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THE MAMMALIAN FAUNA OF THE WHITE RIVER OLIGOCENE

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PART II. RODENTIA

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INTRODUCTION

In March, 1936, Professor Scott requested me to review the rodents and lagomorphs for the monograph of the White River fauna. I was extremely glad to accept this opportunity of studying as a whole the important collections from the White River, which, especially the rodents, have been described in such a fragmentary and cursory manner as to have remained essentially unknown, by comparison with the other orders represented by abundant material in the White River. It has proved convenient to divide this work into two parts, the first dealing with the rodents, the second with the lagomorphs. In addition to providing me with his backing and official sanction in making this study, and a means of publication after it was finished, for both of which I find it difficult to express my extreme gratitude, Professor Scott has also supplied, in the person of Mr. Bruce Horsfall, the artist who has made all of the excellent illustrations embodied in the plates. For the text figures, except where otherwise credited, I must accept the responsibility myself. Professor Scott further assisted me financially from the grants which he had received from the American Philosophical Society, which alone enabled me to finish this study so quickly.

Much of the preliminary work for what is here included was, however, undertaken during 1934–35, when I was Cutting Traveling Fellow in Columbia University. At this time I was enabled to study most of the important collections of White River rodents, and have thus been able to base this review on almost all of the White River collections extant, both in the United States and abroad. I wish to express my thanks at this point to Professor E. H. Barbour of the University of Nebraska, Mr. J. J. Burke of the Carnegie Museum, Professor E. C. Case of the University of Michigan, Dr. C. L. Gazin of the United States National Museum, Dr. Walter Granger of the American Museum, Professor G. L. Jepsen of Princeton University, Professor F. B. Loomis of Amherst, Professor A. S. Romer of the Museum of Comparative Zoology, Dr. Loris Russell of the Canadian National Museum, and Mr. Paul McGrew, of the University of Chicago, all of whom have unreservedly lent me certain of the specimens in their collections, and have expressed willingness for me to include in this study any such material of White River age.

I have found it utterly impossible to write this review without including, both consciously and unconsciously, many ideas suggested to me by other workers in vertebrate palaeontology, and especially by those dealing with rodents. Of these last, I wish particularly to indicate my indebtedness to Dr. Samuel Schaub of the Naturhistorisches Museum of Basle and to Mr. J. J. Burke of the Carnegie Museum. I have absorbed so many ideas from my conversations with these two workers that, although I have tried to give them credit for any suggestions of theirs that have been embodied in the text, I am sure they will recognize many others cropping up without acknowledgment. I wish to express my regret for any such negligences on my part, and to assure them of my deep appreciation of their continued assistance.

In the introduction to the first part of this monograph (p. 7), Scott and Jepsen say that little attention will be paid to species, and no attempt will be made to revise them. So little work has been done on the rodents, however, that it is fairly simple to revise the

described species as well as the genera. In several instances I have been forced to describe new species in order to give even the faintest idea of the diversity of forms actually known from the White River deposits.

It is, of course, true that at any given time a greater number of species of rodents will occupy a given area than of any group of larger mammals, due to the more limited geographic distribution of the individual species of rodents. We should expect, therefore, greater specific diversity among the White River rodents than among, for example, the Oreodonts.

In Pt. I of this work (p. 8) Scott and Jepsen list the number of families and genera of each order of mammals occurring in the White River. They list six families and twelve genera of rodents, whereas I have recognized nine families and nineteen genera of rodents in the following pages. This discrepancy is due to changes in our knowledge of the White River fauna that have come as a result of this study, but too late to be incorporated in the lists of the first part.

The arrangement of the genera within the respective families, as followed in this paper, is a relatively simple matter, there being very general agreement among authors on this point. By and large, I have followed Miller and Gidley (1918) in this respect, the most important instances in which I have differed from them (other than in the placing of genera described since the publication of their classification) being the inclusion of *Prosciurus* among the Sciuravidae instead of among the Paramyidae, and the union of *Adjidaumo* and *Paradjidaumo* with *Eomys* and its relatives to form the Eomyidae. The reasons for these changes are discussed in greater detail below.

When it comes, however, to the arrangement of the families into superfamilial groups, we tread on extremely dangerous ground. I have arranged the families, with greater or lesser certainty, into superfamilies, and these last into suborders. The families grouped in the "Protrogomorpha" represent a stock that is in many respects rather primitive. Its relations, if any, to other rodents have yet to be established. The relationships of the families themselves may well be quite distant, but, for the present at least, they can be grouped in this manner.

By following the system of leaving as *incertae sedis* the rodents of most questionable affinities, and of making no attempt to extend the classification to include forms not found in the White River, the rest of the superfamilial classification will probably arouse few comments, favorable or otherwise.

The most difficult, as well as the most important, point is the grouping of superfamilies into suborders. The "Sciuromorpha" and "Myomorpha" are accepted for the present as being essentially the equivalents of Miller and Gidley's "Sciuroidae" and "Muroidae." Zittel's term "Protrogomorpha" is used for the relatively primitive stock which forms the preponderance of Miller and Gidley's "Dipodoidae." In using these subordinal groupings, it must be remembered that there is no conclusive evidence to establish either that they are natural groups, or that they are not. They are intended merely as convenient tentative categories which may or may not have a genetic significance.

The subordinal names are used instead of Miller and Gidley's superfamilies for three reasons. In the first place, while covering essentially the same ground, they have been in very general usage and antedate Miller and Gidley's terms by some time. Secondly, Miller and Gidley's terms do not conform to the usual method of forming superfamily

names. Lastly, the use of suborders allows the introduction of one additional stage in classification, which I believe to be an item of considerable importance for the present, at least, among the rodents.

The cusp terminology adopted throughout this paper is that suggested by Wood and Wilson (1936), together with the terms for the sulci and valleys invented by Stirton (1935, p. 392).

Order RODENTIA Cuvier

Suborder **PROTROGOMORPHA** Zittel, 1893

Zittel erected this suborder for a group of families which he believed to represent the primitive stock of the order. Since the original publication of this term, it has been generally ignored, and the forms which he included in this suborder have usually been placed among the Sciuromorpha. Miller and Gidley included most of them among their Dipodoidae, of which group they form the backbone. It seems to be impossible to include these families in any of the three generally accepted suborders. They are certainly not "Hystricomorphs"; they have practically nothing in common with the "Myomorphs," and very little with the "Sciuromorphs." Neither can I see any justification for associating them with the Dipodidae. It is obvious, therefore, that they must represent an independent group, for which Zittel's term is available.

Zittel included here the Ischyromyidae (= Paramyidae + Sciuravidae + Ischyromyidae, in the sense in which the terms are now used), Pseudosciuridae, Theridomyidae, Myoxidae, Dipodidae, Aplodontidae, Anomaluridae and Pedetidae. From this list it is at once clear that Zittel's classification is almost identical with that of Miller and Gidley, in so far as its results are concerned. Some of these families, as the Dipodidae, certainly do not belong in the same group as the Paramyidae, Sciuravidae and Ischyromyidae. Others, as the European fossil forms, the Anomaluridae, Myoxidae and Pedetidae, whatever their relationships may be, are fortunately beyond the scope of this paper, and have therefore been neglected. For the time being, the "Protrogomorpha" will be considered as including the superfamilies Ischyromyoidea and Aplodontoidea and the families Paramyidae, Sciuravidae, Ischyromyidae, Cylindrodontidae, ?Protoptychidae, Allomyidae, Aplodontidae and Mylagaulidae.

The suborder may be defined as follows: rodent families in which the masseter has not modified the form of the infra-orbital foramen in any manner; tibia and fibula separate; dental formula $P\frac{1-2}{1}$, $M\frac{3}{3}$. The range is from the lowest Eocene to the Recent, of Europe, Asia and North America, at least. They were much more important in the Tertiary than they are at present.

Superfamily **ISCHYROMYOIDEA**

Primitive rodents, the infra-orbital foramen never transmitting any part of the masseter; masseter in known forms limited in vertical expansion by the infra-orbital foramen; this last high on the face, not having been forced down as in the Dipodidae; cheek tooth pattern based on transverse lophs, rather than on antero-posterior ones as in the Aplodontoidea; skull not extremely flattened.

Families: Paramyidae, Sciuravidae, Ischyromyidae, Cylindrodontidae, ?Protoptychidae and probably others.

Range: Lowest Eocene through the Oligocene. One form from the Pliocene is doubtfully referred here. North America and Asia and probably Europe and Africa.

Family SCIURAVIDAE Miller and Gidley, 1918

This family may be defined as follows: infra-orbital foramen of medium size and low on the rostrum, but not transmitting any part of the masseter; bullae small; upper molars tritubercular or quadritubercular; lower molars with well developed mesoconid; ectolophid not marginal as in Paramyidae; entoconid of molars connected by a crest with mesoconid or ectolophid just posterad of mesoconid.

Range: Middle Eocene to Upper Oligocene of the United States, Oligocene of Canada and Mongolia, with doubtfully referred forms from the Lower Eocene of Wyoming and the Pliocene of Kansas.

Prosciurus Matthew

(Pl. XXIII, Figs. 1, 2 and 4)

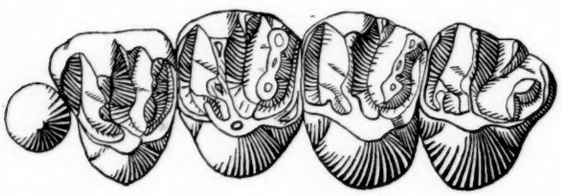
Genotype: *P. vetustus* Matthew, 1903.

The crowns of the teeth are low. The upper molariform teeth have undivided or partly divided protocones, complete protolophs, incomplete metalophs, and large and rounded metaconules, connecting with the protocone only after considerable wear. The lower teeth are rhomboidal rather than square. The talonid is much lower than the trigonid, especially than the metaconid. The anterolophid is continuous with the protoconid and metaconid. The posterior arm of the protoconid curves toward the metaconid, normally reaching it only in the premolar. The mesoconid is rounded. There is a well developed mesostylid on all the teeth. The crest from the entoconid generally unites with the space between the mesoconid and the hypoconid. The valley between the hypolophulid I and the posterolophid is very small and shallow, whereas the central basin is large. The infra-orbital foramen is of the "Protrogomorph" type, being fairly large and low on the face, with no evidence that it transmitted any part of the masseter. The masseter lateralis superficialis had a considerable area of origin on the ventral part of the zygoma. There is a well developed postorbital process, and the bullae are small and squirrel-like. The temporal fossae are likewise small. The masseteric fossa ends below $M\underline{2}$, but is continued anteriorly beneath $M\underline{1}$ by a triangular surface, apparently for the attachment of the masseter, but not truly a fossa. The mental foramen is below and slightly anterior to $P\underline{4}$.

Range: Lower Oligocene of South Dakota, Montana and Saskatchewan; Middle Oligocene of South Dakota, Wyoming and Colorado; Upper Oligocene of South Dakota; Hsanda Gol Oligocene of Mongolia.

Of the upper teeth (Figs. 8–11 and Pl. XXIII, Fig. 1*b*), $P\underline{3}$ is small and merely a simple conical cusp. The other teeth are of about the same size and of the same general pattern. The fourth premolar differs from the molars chiefly in the great expansion of the external portion of the anterior cingulum, in the neighborhood of the parastyle. The protoloph is complete on all the molariform teeth. The metaloph is incomplete in unworn teeth. The protoconule and metaconule are close together, and unite upon wear, though not until after the latter unites with the protocone. In some species, there are crests between the two conules or between the paracone and metacone. The hypocone is poorly developed and is behind the metaloph, which ends at, or just behind, the protocone. The anterior cingulum is broad, the posterior one much narrower, uniting with the metacone. This last has moved to the extreme posterior end of $M\underline{3}$, in which tooth the posterior cingulum is extremely short.

$P\bar{4}$ is almost, but not quite, molariform, the cusps of the trigonid being much closer together than are those of the talonid (Figs. 12 and 18). The anterior arm of the protoconid is continued through the anterior cingulum to the metaconid, forming a well developed anterolophid in all of the molars and a weak crest in the premolar. There is frequently a swelling on this crest near the protoconid. In the premolar, the posterior arm of the protoconid unites with the metaconid; in the molars, except in ?*P. jeffersoni*, it reaches



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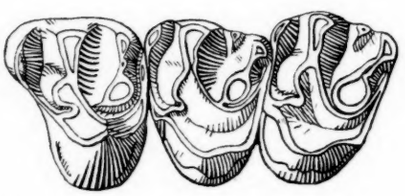

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FIG. 8. *Prosciurus vetustus* Matthew. Holotype. Amer. Mus. No. 9626, P3–M3 left.
FIG. 9. *Prosciurus* cf. *relictus*. Amer. Mus. No. 12,263, P4–M2 left.
FIG. 10. *Prosciurus vetustus* Matthew. M.C.Z. No. 17,279, dP4 left.
FIG. 11. *Prosciurus* cf. *lohiculus*. A.E.W. No. 9052, M3 right, reversed.
FIG. 12. *Prosciurus relictus* (Cope). Holotype. Amer. Mus. No. 5360, $P\bar{4}$–$M\bar{3}$ left.
FIG. 13. *Sciuravus nitidus* Marsh. Holotype. Y.P.M. No. 13,333, M1–3 left.
FIG. 14. *Sciuravus undans* Marsh. Holotype. Y.P.M. No. 13,349, $P\bar{4}$–$M\bar{2}$ right.
FIG. 15. *Tillomys* cf. *parvus*. Y.P.M. No. 13,566, P4–M2 left.
FIG. 16. *Tillomys parvus plicatus* Troxell. Holotype. Y.P.M. No. 13,352, $P\bar{4}$–$M\bar{3}$ right.
All figs. × 10.

about half way from the protoconid to the metaconid, and, in $M\bar{3}$, points posterad rather than toward the metaconid. The mesoconid is a well developed, rounded triangular cusp. It seems never to have any continuations as a mesolophid, although lingual stylids sometimes occur. There is considerable variation in the size of the mesostylids, which is not a wear feature, but whether or not this is a specific character is not clear at present. The hypolophulid I is a long slender crest, usually without any complications other than a slight curve near the middle, and reaches the ectolophid half way between the mesoconid and the hypoconid. This is a very low crest, often being barely visible under the microscope. Its size and shape are such that it tends to be worn flush with the surface of the central basin without forming dentine lakes. There is, however, considerable variation in its size and length. After wear, the entoconid often unites with the middle of the posterolophid, as described below for *P. relictus* (see p. 168). This worn effect simulates what is the normal condition of $P\bar{4}$ in *Sciuravus undans* (Fig. 14), where the entoconid is connected with the posterior cingulum, whereas in its molars, the conditions are as in unworn molars of *Prosciurus*. In this character of the premolar, *Tillomys* (Fig. 16) is nearer to *Prosciurus* than is *Sciuravus*, the arrangement of the hypolophulid I being essentially identical in these two forms. In the lack of a mesoconid, the emphasis of metalophulid II, and the reduction of metalophulid I, *Tillomys* is quite distinct from *Prosciurus*. *Pauromys* (Fig. 65), which seems to be an aberrant sciuravid, is still further removed from *Prosciurus*. The variability of the connections of the entoconid of *Prosciurus*, dependent on wear, suggests, as would be expected on other accounts, that the exact relationships of the hypolophulid are of less phylogenetic importance than certain of the differences between *Prosciurus* and *Tillomys*, such as the absence of the mesoconid in the latter.

In *Prosciurus*, the hypolophulid I rather has the appearance of being an outgrowth from the entoconid, having no genetic connection with the hypoconid. If this is correct, it would represent an entirely different mode of crest formation from that in the Cricetidae, Eomyidae, Cylindrodontidae or Ischyromyidae. The posterolophid is long and slender, reaching to the lingual margin of the tooth, but not uniting with the entoconid. This separation is probably a secondary development. Generally the hypoconulid is not visible, though it sometimes occurs as a rather indistinct swelling, and rarely as a distinct cusp. It is usually merely an irregularity in the course of the posterolophid. The hypoconid is at the extreme posterior end of the tooth. The distance between the hypoconid and the metaconid is much greater than that between the protoconid and entoconid, giving the tooth a decidedly rhombic outline.

The skull is unfortunately known only from anterior fragments and a posterior section. If worn teeth are of any value in indicating relationships, however, these two parts belong to the same genus. The anterior region (represented only by the palatine portion of the maxilla and the lower part of the infra-orbital foramen) is that of a typical ischyromyoid, while the braincase is very suggestive of the Sciuridae. The infra-orbital foramen is large and very low on the face, the lower branch of the maxillary root of the zygoma is almost horizontal, and the masseter is limited to a deep groove on the ventral surface of the zygoma (Pl. XXIII, Fig. 4). It thus is quite different from what is seen in any of the sciuromorphs. The rear half, on the contrary, is very suggestive of the Sciuridae (Pl. XXIII, Figs. 1, 1*a*, 1*b*). There is a very strong postorbital process, larger than in *Sciurus*. The bullae are small as in *Sciurus*, being much smaller than in *Ischyromys*, but are fully ossified, thus being more

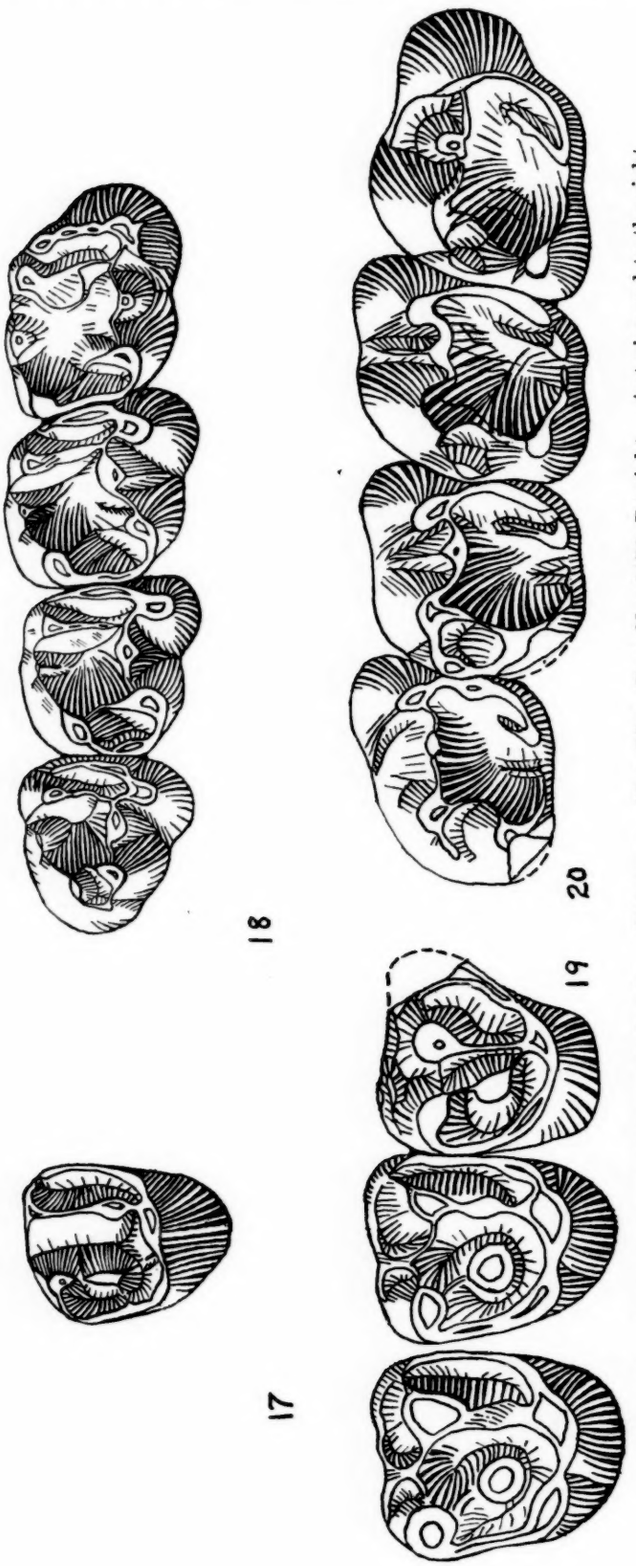


Fig. 17. *Prosciurus saskatchewaensis* Lambe. Holotype. Nat. Mus. Can. No. 6479, $P\frac{4}{4}$ right. Anterior end to the right.
Fig. 18. *Prosciurus* cf. *saskatchewaensis*. Amer. Mus. No. 8750, $P\frac{4}{4}$–$M\frac{3}{3}$ left.
Fig. 19. *Prosciurus* sp. P.U. No. 14,242, $M\frac{2}{2}$–$P\frac{4}{4}$ right. Anterior end to the right.
Fig. 20. *Prosciurus jeffersoni* (Douglass). Holotype. Carn. Mus. No. 736, $P\frac{4}{4}$–$M\frac{3}{3}$ right.
All figs. × 10.

progressive than those of *Sciuravus*. Their shape is almost identically that of *Sciurus*, with a deep fossa on the anterior side. The skull is low and fairly flat, instead of being expanded and arched as in *Sciurus* and *Sciuravus*. The post-glenoid foramina are much smaller than in *Sciurus*, being about as in *Sciuravus*. The inter-parietal is fused with the parietal. The temporal crests are lyre-shaped, beginning on the postorbital processes, and reaching the occipital surface without quite meeting. The area between them is flat. This is a striking difference from both *Sciurus* and *Sciuravus*, in both of which the temporal crests unite to form a sagittal crest, and suggests that the temporal muscle was unusually weak. The postorbital processes are distinctly further forward than in *Sciurus*, being clearly in front of the fronto-parietal suture, the process being formed entirely from the frontal, instead of from both bones, as in the Sciuridae. There is, of course, no postorbital process in *Sciuravus*. The occiput is higher in *Sciurus*, correlated with the more swollen brain case. The foramen magnum of *Prosciurus* is round, instead of high and triangular as in *Sciurus*, and the occipital condyles were nearly vertical instead of nearly horizontal as in the squirrel. The paroccipital processes seem to have been similar in the two forms. The palate ends just behind $M\underline{3}$.

This specimen shows many striking similarities to the skull of *Sciurus*. Until one specimen shall be found, showing the entire skull, it will be impossible to prove definitely that this squirrel-like postorbital portion of a skull belongs to the same animal as the entirely un-squirrel-like infra-orbital region of *Prosciurus*. If two distinct forms are represented, however, it is one of the most striking instances of parallelism of tooth pattern known anywhere among the Rodentia—and parallelism is one of the most striking features of the whole order (compare Figs. 8–9 with Pl. XXIII, Fig. 1*b*). It is clear, however, that the rear of the skull is not identical with that of *Sciurus*. The shape, size, position and make-up of the postorbital process, the position of the condyles, and the shape of the foramen magnum would all appear to be rather fundamental characters, not likely to change very easily. For the time being, therefore, this skull is referred to *Prosciurus*, which is considered as representing an extremely close parallel in many characters to the Sciuridae by a member of the Ischyromyoidea. It is possible, of course, that this cranium belongs to a primitive, and quite aberrant, sciurid. The earliest known sciurid skulls, from the John Day, however, have teeth which have definitely acquired the pattern exhibited by the modern members of the family, to which the tooth pattern of *Prosciurus* could not possibly be ancestral.

The masseteric fossa of the mandible is different from anything with which I am familiar. The main part of the fossa ends below the anterior end of $M\overline{2}$. There is a small flat area, part of the insertion of the masseter, extending as far forward as the middle of $M\overline{1}$ (Pl. XXIII, Fig. 2). The mental foramen is only slightly anterad of $P\overline{4}$.

Matthew (1903) described *Prosciurus* as a subgenus of *Sciurus*, considering that the pattern of the cheek teeth was sufficiently distinct to warrant subgeneric distinction, but no more. Lambe (1908) in describing the Cypress Hills fauna, indicated that the form he was describing as *Sciurus saskatchewaensis* was probably distinct from *Sciurus*, though a new genus could not be established with the material then available. By 1910 Matthew had decided that this form was worthy of full generic rank, and said (1910, p. 63) that "the anterior margin of the masseteric fossa is under $M\overline{2}$ as in *Paramys*, *Ischyromys*, etc., instead of under $P\overline{4}$ or $M\overline{1}$ as in Sciuridae. This appears in the types of *S. relictus* and

wortmani Cope and in two undescribed jaws from the White River. The relations of the infra-orbital foramen in the type of *S. vetustus* were apparently as in the Ischyromyidae and certainly not as in the Sciuridae. From these indications I judge that these species retained the primitive construction of the antorbital region." "*Sciurus*" *wortmani* Cope, however, is quite distinct from *Prosciurus*, being a true sciurid. Matthew, of course, used the term Ischyromyidae to include the forms separated by Miller and Gidley into Paramyidae, Sciuravidae and Ischyromyidae.

Miller and Gidley (1918) include *Prosciurus* among the Paramyidae. It differs sharply from the members of that family, however, in possessing mesostylids on all the teeth; in the large size and central position of the mesoconid; in the strong ectolophid; in the possession of a hypolophulid I, whereas there is no hypolophulid of any sort in *Paramys;* in *Paramys* the entoconid unites with the hypoconid via the posterior cingulum, whereas in *Prosciurus* the valley between the entoconid and the cingulum is entirely open at the lingual end; the infra-orbital foramen is distinctly reminiscent of that of *Sciuravus* and distinct from that of *Paramys* in the size of the area of origin of the masseter on the ventral surface of the zygoma. Since *Prosciurus* agrees with *Sciuravus* in all of these characters, it seems evident that it should be included in the same family as the Bridger form, the chief significant difference being that the Oligocene form has little or no hypocone in the upper molariform teeth, while the hypocone is widely separated from the protocone in *Sciuravus*. This apparently more primitive pattern occurring in the later form is perfectly reasonable, and does not indicate progressive simplification, certain recent authors to the contrary notwithstanding, since there is no evidence that *Prosciurus* is a descendant of *Sciuravus*.

Prosciurus, then, is a primitive sciuravid, with low crowned teeth, weak hypocone, and lower teeth with a large central basin, which is being invaded by cusps and crests from the periphery. In the size of the central basin, *Prosciurus* is quite distinct from *Sciuravus*, in which the central basin is of relatively small size. If *Paramys* is the primitive type, *Prosciurus* is more primitive in this character than is *Sciuravus*. The trigonid is definitely higher than the talonid, though not as much so as in the Bridger members of the family.

Peterson (1919) described as *Prosciurus* (?) *robustus* a form from the Myton member of the Uinta. In size this is very much larger than any member of *Prosciurus*. It is difficult to determine the pattern from Peterson's figure (op. cit., Fig. 6), but there does not seem to have been a hypolophulid; the hypoconulid seems to have been very robust, and there seems to have been a large ectostylid, all of which characteristics separate it from *Prosciurus*, and tend as suggested by Gidley in a footnote to Peterson's paper, to associate it with members of the Paramyidae. This form can safely be disregarded in considering the ancestry of *Prosciurus*.

The lower cheek teeth of *Prosciurus* have many similarities to those of *Sciuravus*, more so than to any other of the Bridger rodents with which I am familiar (see Figs. 12, 14, 18 and 20). The only significant differences seem merely to be primitive characters retained by one form or the other. In the upper teeth, on the contrary, the difference between the two genera is striking, *Sciuravus* having a well developed hypocone, with the protoloph and metaloph completely separated, the median valley running all the way across the tooth. The upper teeth of *Tillomys* are much closer to those of *Prosciurus*, matching them very closely in many respects (see Figs. 8, 9 and 15). In view of this, it is, of course, impossible to derive *Prosciurus* from either genus, though it is clear that

it is closely related to the Bridger forms. There are sufficient similarities so that we may consider ourselves justified, for the present, in regarding *Prosciurus* as descended from forms similar to the Middle Eocene stock represented by *Sciuravus*, *Tillomys*, *Taxymys*, *Colonomys* and *Pauromys*. Of these, the last three are distinctly further from *Prosciurus* than are the first two.

Prosciurus vetustus Matthew

Sciurus (*Prosciurus*) *vetustus*, Matthew 1903.
Prosciurus vetustus Matthew, Matthew 1910.

(Figs. 8 and 10; Pl. XXIII, Fig. 4; Matthew, 1903, Fig. 9; and Osborn, 1907, Fig. 105)

Holotype: Amer. Mus. No. 9626, maxilla with P3–M3 left.

The cheek teeth are relatively long antero-posteriorly. P4, the smallest of the molariform teeth, has a small parastyle and a mesostyle. The metalophs of all the cheek teeth have two metaconules.

This species, as can be told from the respective diagnoses, differs very slightly from *P. relictus*, as represented by Amer. Mus. No. 12,263 and M.C.Z. No. 17,279, fragmentary maxillae. Furthermore, there is little difficulty in bringing the holotype of *P. vetustus* into occlusion with that of *P. relictus*—no more than might easily occur in members of the same species. Since, however, there are certain differences between the two forms, and since our knowledge of *Prosciurus* is as incomplete as is the case at present, it seems best to retain the two species for the time being. In this species, the metaconules are double on all the teeth, whereas in *P. relictus*, they are single on M1, and nearly so on P4 and M2, and they are also single on the holotype of *P. saskatchewaensis*. The palatine reaches on the palate to the anterior end of M2. The posterior end of the zygomatic process curves out by P3. The masseter was limited to the ventral face of this process. The infraorbital foramen is very low on the face, lying immediately above the narrow zygomatic process.

Measurements of *Prosciurus vetustus*

	Holotype, Amer. Mus. No. 9626	*Mus. Comp. Zool. No. 17,279*
P3–M3	7.67 mm.	—
P3 a-p	0.90	—
transverse	0.96	—
P4 a-p	1.70	d1.88 mm.
width protoloph	2.23	d1.97
width metaloph	2.20	d2.05
M1 a-p	1.73	2.02
width protoloph	2.40	2.67
width metaloph	2.32	2.46
M2 a-p	1.80	1.98
width protoloph	2.45	2.58
width metaloph	2.17	2.48
M3 a-p	1.93	—
width protoloph	2.15	—
width metaloph	2.00	—

d = deciduous tooth.

Matthew (1903, p. 213) was mistaken in thinking there was a significant difference in size between this species and *P. relictus*, since, although there is a slight difference in size (see tables, pp. 167, 168), it is well within the limits of individual variation, and hence without significance.

Range: Lower Oligocene of Pipestone Springs, Montana, and Lower Oligocene of South Dakota.

Prosciurus relictus (Cope)

Paramys relictus, Cope 1873*b*.
Sciurus relictus (Cope), Cope 1874.
Prosciurus relictus (Cope), Matthew 1909 (in Osborn and Matthew, 1909).

(Fig. 12; Pl. XXIII, Fig. 2; and Cope, 1884, Pl. LXV, Figs. 35, 35*a*, 35*b* and 35*c*)

Holotype: Amer. Mus. No. 5360, lower jaw with $P\bar{4}$–$M\bar{3}$ left.

The molariform teeth are of nearly the same size throughout. There is an ectostylid, and the metalophulid II is incomplete, on all the molars. Usually there is only a single metastyle.

It is difficult to distinguish this species with certainty from *P. vetustus*, as they are of about the same size, are in similar stages of evolution, and the holotypes are not comparable. The first three molariform teeth are of uniform length, and the third molar is not greatly longer than the others (see Fig. 12 and table of measurements).

The protoconid of $P\bar{4}$ has a short anterior arm, which sometimes expands into a slight anteroconid. The hypolophulid I is clearly shown on all the teeth when unworn. After a little wear, on $P\bar{4}$ and $M\bar{1}$ at least, the crest is entirely worn away across the central valley, and the entoconid unites by a short crest with the posterior cingulum, near the lingual end of the latter. This elimination of the central part of the hypolophulid I is permitted by the extremely low nature of that part of the crest, which is here barely more than a wrinkle on the surface of the basin, as has already been explained.

MEASUREMENTS OF *Prosciurus relictus*

	Holotype, Amer. Mus. No. 5360	*Univ. Mich., no number*	*U.S.N.M., no number*
$P\bar{4}$–$M\bar{3}$	7.70 mm.	7.25 mm.	—
$P\bar{4}$ a-p	1.81	1.80	—
width metalophid [1]	1.43	1.24	—
width hypolophid [1]	1.79	1.67	—
$M\bar{1}$ a-p	1.70	1.62	1.68 mm.
width metalophid	1.71	1.48	1.50
width hypolophid	1.88	1.62	1.67
$M\bar{2}$ a-p	1.94	1.62	1.75
width metalophid	1.90	1.71	1.83
width hypolophid	2.00	1.77	1.88
$M\bar{3}$ a-p	2.35	2.17	2.22
width metalophid	1.93	1.80	1.82
width hypolophid	1.77	1.60	1.47

[1] These terms are used in all tables, whether the crests are metalophid and hypolophid or metalophulid and hypolophulid.

In the holotype, the mesostylids are small and rounded. In other specimens, they are elongate transversely, and in one specimen from Douglass, Wyoming, in the National Museum, reach nearly to the ectolophid.

Range: Middle Oligocene of Colorado, South Dakota, Nebraska and Wyoming.

Prosciurus cf. **relictus**

A maxilla with P4–M2 left, from the Leptauchenia Beds west of Silas Ranch, Pass Creek, South Dakota, Amer. Mus. No. 12,263, is tentatively referred to this species. It is of correct size to belong to this form, though it differs in some details from the Middle Oligocene maxillae that seem to belong with *P. relictus* mandibles. This form is quite similar to *P. vetustus*, differing chiefly in the presence of strongly developed lingual cingula, the absence of connections between the protocone and the metaconule until after extreme wear, and the small size of the mesostyle. The double metaconules of *P. vetustus* seem to have been reduced essentially to one, though there are minute extra ones on P4 and M2 (see Fig. 9). Otherwise the two forms are essentially identical, in spite of having been separated by almost the entire Oligocene.

MEASUREMENTS OF AMER. MUS. NO. 12,263

	P^4	M^1	M^2
Antero-posterior	1.98 mm.	1.80 mm.	1.76 mm.
width protoloph	2.40	2.30	2.40
width metaloph	2.35	2.20	2.32

Prosciurus saskatchewaensis (Lambe)

Sciurus ? saskatchewaensis, Lambe 1908.

Prosciurus saskatchewaensis (Lambe), Russell 1934.

(Fig. 17 and Lambe, 1908, Pl. 8, Figs. 16 and 17)

Holotype: Nat. Mus. Can. No. 6479, M1 ? right.

This is a relatively primitive *Prosciurus*, though much larger than either *P. vetustus* or *P. relictus*. There is no lingual cingulum, only one metaconule, no mesostyle, and an incipient crest connecting the metaconule and the posterior cingulum. Very little can be told about the holotype more than the characters listed above.

Lambe seems to have been correct in calling this a right upper molar, and Russell (1934, p. 57) to have been mistaken in considering it as the fourth premolar. The parastyle and anterior cingulum are nowhere near large enough to be that tooth.

Another tooth, in the author's private collection, A.E.W. No. 9057, seems to be M2. It adds nothing to the information given above, and is badly waterworn.

MEASUREMENTS OF *Prosciurus saskatchewaensis*

	Holotype, Can. Nat. Mus. No. 6479 M1?
Antero-posterior	2.27 mm.
width protoloph	2.35
width metaloph	2.98

Range: Lower Oligocene of the Cypress Hills, Saskatchewan.

Prosciurus cf. **saskatchewaensis**

A lower jaw, Amer. Mus. No. 8750, with $P\bar{4}$–$M\bar{3}$ left, from the Cedar Creek Beds, is tentatively referred to this species. This is the jaw referred to by Matthew (1901, p. 357) as an example of *P. wortmani* from the Cedar Creek. It is about the right size to belong to *P. saskatchewaensis*. As was indicated by Lambe (1908, p. 55), *P. saskatchewaensis* lacks the sharply differentiated parastyle of *P. vetustus* and *P. relictus*, the antero-external enamel crest being essentially continuous with the paracone. The absence of the parastyle is perhaps correlated with the absence of the ectostylid, no trace of this cusp being found in the Cedar Creek jaw (Fig. 18).

$P\bar{4}$ is much reduced, being shorter than in *P. relictus*, and with the metalophid distinctly narrower. $M\bar{1}$ also differs from *P. relictus* in having a complete metalophulid II, almost as high as the marginal crest. There is also a complete, though low, anterior marginal crest of $P\bar{4}$. The metalophulid II is essentially complete on $M\bar{2}$, and much more so on $M\bar{3}$ than in *P. relictus*. It also runs in much more the normal direction, rather than trending toward the rear. The mesostylids are closely united with the metaconids, being connected by a continuous crest. The hypolophulid I is clearly shown, probably because this specimen is unworn. The incisor is flat and rounded laterally as in *P. relictus*.

The masseteric fossa is identical in shape with that of *P. relictus*, except that the anterior flat surface extends further forward, reaching to the middle of $P\bar{4}$. The mandibular foramen is high on the ascending ramus.

This specimen seems more *Tillomys*-like than is *P. relictus*.

Carn. Mus. No. 539 consists of two lower jaws from the Oreodon Beds, Badland Creek, Sioux County, Nebraska. One of these is conspecific with the present form, the other referable to *P. relictus*.

MEASUREMENTS OF *Prosciurus* CF. *saskatchewaensis*

	Amer. Mus. No. 8750		*Amer. Mus. No. 8750*
$P\bar{4}$–$M\bar{3}$	10.40 mm.	$M\bar{2}$ a-p	2.57 mm.
$P\bar{4}$ a-p	2.48	width metalophid	2.52
width metalophid	1.93	width hypolophid	2.73
width hypolophid	2.51	$M\bar{3}$ a-p	3.03
$M\bar{1}$ a-p	2.41	width metalophid	2.46
width metalophid	2.26	width hypolophid	2.36
width hypolophid	2.46		

Prosciurus aff. ? **saskatchewaensis** Lambe

(Pl. XXIII, Figs. 1, 1*a*, 1*b*)

The rear of a skull, Amer. Mus. No. 1429, from the Oreodon Beds of South Dakota represents a form close to this species. The snout is missing, and the only teeth present are $M\underline{1}$–$\underline{2}$ right and left, all badly worn. They agree in size with those of *P. saskatchewaensis*, and are tentatively referred here. The characters of this specimen are discussed above, in the generic consideration.

Prosciurus sp.

(Fig. 19)

A maxilla, P.U. No. 14,241, with P4–M3 right, belongs to a large species, apparently distinct from the last mentioned one. This differs from all other species of the genus in the strong ectoloph connecting the paracone and metacone, via the mesostyle. This last is a good-sized cusp. There is a strong external cingulum on P4, and weaker ones on M1–2. Another specimen, P.U. No. 14,242, is also referred here. The protoconule is small, the metaconule enlarged, being as large as the paracone or metacone. The hypocone is very small, appearing only as a swelling of the posterior cingulum. This may be conspecific with the form identified as *Prosciurus* cf. *saskatchewaensis*, but probably is not.

MEASUREMENTS OF *Prosciurus* sp.

	P.U. No. 14,242		*P.U. No. 14,242*
P4 a-p	c2.85 mm.	M2 a-p	2.89 mm.
width protoloph	2.89	width protoloph	3.47
width metaloph	3.08	width metaloph	3.42
M1 a-p	2.69		
width protoloph	3.50		
width metaloph	3.41		

If Matthew was correct in deriving *Meniscomys* from *Prosciurus* (Matthew, 1910, phylogenetic chart), a derivation which seems highly questionable, this form stands the nearest to *Meniscomys* of any known species.

Horizon: Brulé.

Prosciurus aff. **lohiculus** Matthew and Granger, 1923

(Fig. 11 and Matthew and Granger, 1923, Fig. 8)

A single tooth from the Cypress Hills, A.E.W. No. 9052, is tentatively referred to this species. It agrees with the holotype and only known set of upper teeth of the Mongolian form in the extremely high crowns, development of a continuous external wall, blocking the three very deep valleys; the absence of a mesostyle; and the presence of anastomoses between the metaloph and the posterior cingulum. As this tooth is an M3, a tooth which is absent in the Mongolian specimen, direct comparison is impossible. There were, however, connections between the protoconule and the anterior cingulum (see Fig. 11), which are not present on the other teeth of the Mongolian form. This specimen is clearly distinct from *P. saskatchewaensis*, in the anastomoses between the lophs and the cingula, in the complete external wall, and in the extremely high crown. This form, together with the Mongolian one, may be sufficiently distinct to warrant generic separation from *Prosciurus*, when better known. The Cypress Hills specimen is certainly not conspecific with the Mongolian one, but this cannot be demonstrated with the available material. The connection between the protoconule and the metaconule does not seem as fully developed as in *P. lohiculus*. A crest is present across the median valley, but it is incomplete, instead of being complete as in the latter form. The crown is 2.86 mm. high buccally and 1.75 lingually. The tooth is 1.97 mm. long, the protoloph is 2.52 and the metaloph 2.36 mm. wide. This specimen may be referable to *Ardynomys* rather than to *Prosciurus*.

Range: Lower Oligocene of the Cypress Hills, Saskatchewan.

?Prosciurus jeffersoni (Douglass)

Sciurus jeffersoni, Douglass 1902.

Prosciurus jeffersoni (Douglass), Matthew 1909 (in Osborn and Matthew, 1909).

(Fig. 20)

Holotype: Carn. Mus. No. 736, lower jaw with $P\overline{4}$–$M\overline{3}$ right.

The crests from the entoconids are incomplete, and tend to unite with the hypoconulid rather than with the hypoconid or ectolophid. The anterior cingulum cusp is well developed. The two crests between the protoconid and the metaconid are of almost equal development. The hypoconulid is small. The animal is one of the largest species referred to this genus.

The pattern of the cheek teeth of this form is strikingly different from that of other known members of the genus, and may warrant its separation from them. The entire absence of a complete hypolophulid I is obviously a primitive character, uniting this form with certain of the more primitive Eocene forms, though separating it from *Tillomys* and *Sciuravus*. Whether this is a representative of the primitive stock from which the other forms of *Prosciurus* have been derived, or whether it is a member of another line of sciuravids that has exhibited great parallelism to *Prosciurus*, or whether the lack of a complete hypolophulid I is a secondary development, indicating reversal of evolution, cannot be determined at present. If the first is the correct interpretation, there is no known rodent later than Lower Eocene from which this group could have been derived. The double crests of the trigonid would seem to be primitive retentions, and might indicate special affinities with *P.* cf. *saskatchewaensis*.

The mandible is that of a typical *Prosciurus*, with the same type of masseteric fossa as in the other species.

The presence of this form in the lowest Oligocene strongly suggests that this is the ancestral stock of the genus, though, of course, it by no means demonstrates it. If this is correct, it would mean that *Prosciurus* has had an ancestry entirely distinct from that of any other known rodent since the Lower Eocene, and would thus be a stock quite widely separated from the other sciuravids, though probably still referable to that family.

Range: Lower Oligocene of Pipestone Springs, Montana.

MEASUREMENTS OF *Prosciurus jeffersoni*

	Carn. Mus. No. 736 Holotype		*Carn. Mus. No. 736 Holotype*
$P\overline{4}$–$M\overline{3}$	12.04 mm.	$M\overline{2}$ antero-posterior	2.78 mm.
$P\overline{4}$ antero-posterior	2.94	width metalophid	3.24
width metalophid	2.47	width hypolophid	3.24
width hypolophid	2.82	$M\overline{3}$ antero-posterior	3.84
$M\overline{1}$ antero-posterior	2.70	width metalophid	3.16
width metalophid	2.95	width hypolophid	2.78
width hypolophid	3.11		

Certain rodents from the John Day have sometimes been referred to *Prosciurus* under the names of *P. wortmani* and *P. ballovianus*. These forms have the typical sciurid tooth

pattern and the typical sciurid zygomasseteric construction, as has been pointed out by Matthew (1910, p. 63), so there can be no doubt that Cope's original reference of them to *Sciurus* is much more nearly correct than the subsequent references to *Prosciurus*. All of the John Day specimens that I have seen which have been identified as *Prosciurus* turn out to be typical sciurids. Stock (1920) described a lower jaw from the Oligocene of California, which he referred to the Sciuridae. I have not seen this specimen, but it may have been a *Prosciurus*. If it is a true sciurid, it is one of the oldest. Wilson's form from the Sespe (Wilson, 1934, Pl. I, Fig. 3) is likewise a typical sciurid. The genus *Prosciurus*, then, must be limited for the present to forms from the Oligocene of the Great Plains and the Hsanda Gol Oligocene of Mongolia.

Family Ischyromyidae Alston 1876

This family may be defined as primitive protrogomorphs with cheek tooth pattern based on two main transverse crests and anterior and posterior crests. The cheek teeth are brachydont to mesodont. There is no mesocone or mesoconid. The teeth have the metalophulid II. The masseter never passes through the infra-orbital foramen. The masseteric plate of the zygoma varies from non-existent, with the masseter arising from the ventral surface of the arch, to fairly broad and sub-sciuroid in appearance. In habitus, these forms were heavy, slow-moving and sub-fossorial.

Range: Oligocene and uppermost Eocene of North America.

Genera: *Pareumys, Ischyromys* and *Titanotheriomys.*

Ischyromys Leidy

(Pls. XXIII, XXV and XXVI)

Ischyromys, Leidy 1856.

Colotaxis, Cope 1873*a*.

Gymnoptychus, Cope 1873*c* (in part).

Genotype: *Ischyromys typus*, Leidy 1856.

Ischyromys has a reduced anterior cingulum on the upper cheek teeth. The lower teeth are all of essentially uniform width. The temporal crests unite just behind the orbit to form a long sagittal crest. The skull is fairly high in lateral view. The pre-orbital portion of the skull is fairly long. The infra-orbital foramen and the zygoma are usually of the typical protrogomorph type, but sometimes there is a broad maxillary plate below the foramen. The anterior face of the zygoma is more nearly vertical than in *Titanotheriomys*. There is a broad area for the masseter on the ventral surface of the zygoma. The occiput is vertical. The skeleton is subfossorial to ambling.

Range: Entire Oligocene (Pipestone Springs to Leptauchenia Beds) of the Great Plains province of the United States and Canada.

The skull of *Ischyromys* is long and low, with the basicranial axis almost absolutely straight. The pre-orbital portion is about a third the length of the skull, but, in immature individuals, such as S. D. School of Mines No. P293, the snout is longer and more slender. The postorbital constriction lies almost exactly at the middle of the skull, there being close agreement in all these points with *Aplodontia*. The eyes were small and high on the skull, looking distinctly upwards, as in *Paramys*, rather than forward and outward as in the squirrel, or in *Sciuravus*, the eyes of which were large and squirrel-like in their position. An

arrangement similar to that of *Ischyromys* occurs in *Cylindrodon* and *Palaeocastor*, as well as in *Aplodontia*, but not in *Eutypomys*, which is more like the squirrels than the beavers in this respect. Correlated with the small size of the eyes, *Ischyromys* has very large bullae, about twice as large proportionately as those of the squirrel, and even larger proportionately than in *Paramys*, where, however, they are poorly ossified. They are larger than in *Aplodontia*, in which both the bullae and the meatal tubes are quite different in shape from what we see in *Ischyromys*.

Coues' description (1877, p. 565) of the snout of *Aplodontia*, "The rostrum is stout . . . , approximately cylindrical. . . . The nasal bones are truncate anteriorly and do not project beyond the plane of the incisive alveoli" fits *Ischyromys* very well.

The nasals of *Ischyromys* are long and slender, reaching as far caudad as the beginning of the orbit, and extending very slightly anterad of the incisors. Their widest point is near the anterior end, whence they taper gradually to the rear. The anterior ends of the frontals form a nearly straight line across the skull, at the level of the anterior end of the orbit. All of these conditions agree exactly with those in *Aplodontia*. The temporal crests arise from the frontal near the middle of the orbit, and converge rapidly to form a strong sagittal crest. The lacrymal is fairly large, almost separated from the frontal, in dorsal view, by the ascending process of the maxillary, and is quite different from that of *Aplodontia*, where it is more normal in its relationships. The posterior ends of the frontals are carried well back along the midline, forming a deep notch in the anterior margin of the parietals. This notch is deeper and more triangular than in *Aplodontia*. Laterally, the parietals extend essentially to the level of the post-orbital constriction. Posteriorly, also, the parietals are divided by the large, sub-triangular inter-parietal, a bone of which I could find no trace even in a young *Aplodontia*, the sutures of which were still wide open. The lateral edges of the parietal are almost straight. The postero-lateral tips of the bone come into contact with the supra-occipital, which forms a narrow border along the posterior edge of the dorsum of the skull. In *Aplodontia*, due to the absence of a separate inter-parietal, the parietal and supra-occipital are in contact for the entire width of the former. The relative length of the braincase and of the orbit varies considerably in *Ischyromys* from species to species.

The zygomata diverge gradually to the rear, and are at their farthest from the midline just anterad of the glenoid. This is almost exactly the same as the condition in *Aplodontia*. There is a distinct post-orbital process of the malar, even though it is small, and a strong zygomatic process of the squamosal, extending for about a third of the length of the zygoma, along its median surface, in both forms. The malar is quite heavy, its anterior end reaching almost to the level of the infra-orbital foramen, its posterior end reaching the glenoid and forming the lateral margin of that fossa. There is a large temporal foramen at the dorsal margin of the squamosal, forming a notch in this bone just below the parietal. This opening is quite small in *Aplodontia*.

In lateral view, the top of the skull is slightly arched, the top of the arch being formed by the parietal over the cerebral hemispheres. The skull falls down sharply over the cerebellum at the level of the inter-parietal. The zygoma is almost horizontal. The similarity of this view to *Aplodontia* can again be illustrated by a quotation from Coues (1877, p. 566). "The profile of the skull . . . exhibits the remarkable flatness and approximate straightness, horizontality, and parallelism of the upper and under outlines, to which the planes of the occiput and of a tangent to the incisors and the ends of the nasals are both

perpendicular. Along the top of the skull there is a slight bulge in the outline of the parietals, and an equally slight depression over the orbits, whence the profile of the rostrum slopes slightly downward to the end of the nasals. The occiput is perpendicular. . . ."

The lacrymal forms a considerable part of the anterior end of the orbit. The frontal extends about halfway down into the orbit. It does not seem to contain an ethmoid foramen, whereas one is present in *Aplodontia*. At the level of the postorbital constriction are two large foramina, close together near the top of the orbitosphenoid, which seem to be the optic foramen and the foramen lacerum anterius. The latter seems to be united with the foramen rotundum in *Aplodontia*. There is a small sphenopalatine foramen near the base of the alisphenoid, not present in the sewellel, in front of the optic foramen. The foramen ovale is quite large, as in *Aplodontia*, and all the other foramina of this region are confluent with it. There is a large canal, covered by a broad flat plate of bone, arising from the ectopterygoid and extending to the squamosal. There is a similar canal in *Aplodontia*, though it is not as long, that in *Ischyromys* extending posteriorly almost to the bulla. The pterygoid fossa is quite large, the two pterygoid plates being very well developed. The ectopterygoid is continued posteriorly and lies flat against the side of the bulla. The pterygoids are not so well developed in *Aplodontia*.

The bulla is large and rounded and shows no separation between ecto- and ento-tympanic. The meatus is at the postero-dorsal edge of the bulla, and opens postero-dorsally. There is a distinct lip along the anterior side of the meatus. The posterior border of the meatus is formed by a swelling of the bulla, which is not really a lip as yet. The meatus itself is quite small. The paroccipital and mastoid processes are likewise small. This is quite different from the small bulla of *Aplodontia*, with its long, tubular meatus, reaching as far laterad as the edge of the zygoma.

The mastoid is fairly large on the posterior surface of the skull, and is distinctly bullate, being very slightly separated from the tympanic bulla—in fact, the only separation is the narrowing of the bone between the paroccipital and mastoid processes. The mastoid of *Aplodontia* does not seem to be bullate.

The occiput is higher, narrower and more squirrel-like than is that of *Aplodontia*, in which form it has suffered particularly from the dorso-ventral compression of the skull, so that it is extremely broad and low.

The foramen magnum is almost rectangular, its lateral margins being formed by the condyles, which are weakly developed on the ventral surface of the foramen. The upper side of the foramen is almost horizontal. The supra-occipital is large and coarsely corrugated, indicating the attachment of powerful neck muscles, which is again reminiscent of *Aplodontia*, the neck muscles of which are equally powerful.

The hard palate is quite short, ending by the rear of M$\underline{2}$, thus differing from *Aplodontia*, where it ends well behind M$\underline{3}$. The anterior palatine foramina are fairly small, as in *Aplodontia*, but some little distance from the incisors. The posterior palatine foramina are very small, also as in the sewellel. The pterygoids form a heavy ridge for some distance behind the end of the hard palate before they divide into the ecto- and ento-pterygoids, again suggesting *Aplodontia*.

The brain is fairly large and quite simple. The cerebral hemispheres seem to have been absolutely smooth, and not to have overlapped either the cerebellum or the olfactory lobes at all. They were distinctly long and narrow. The cerebellum was large. The

brain is much more slender than that of the sewellel, the brain of which has partaken of the general transverse expansion of the skull (Pl. XXIII, Fig. 5).

The lower jaw is long and slender, with a very large ascending ramus. The coronoid is large and high and recurved, extending back above the condyle. It is broader basally but tapers more than in *Aplodontia*. Neither is its anterior face as nearly vertical as in the latter. The angle is large and broad, with its lower surface curved somewhat inward, delimiting the large pterygoid fossa. It shows no signs of the highly folded angle of *Aplodontia*, with neither the extensive lateral process nor the equally extensive inversion. The anterior end of the masseteric fossa does not make a heavy process as in *Aplodontia*. There is a small fossa just behind the symphysis, as in *Aplodontia*, but much smaller than that in *Eutypomys*. The mandibular foramen opens backwards, just behind and well below $M\underline{3}$. The mental foramen is below the diastema, as in *Aplodontia*. The jaw is deeper under the diastema than in the recent genus.

There is considerable variation within the genus in the incisors, which does not seem to be wholly connected either with age variations or with the various species listed below. Two snouts from the same locality (M.C.Z. Nos. 17,538 and 17,540 from Cottonwood, Pass, Big Badlands) agree in all respects except the incisors. The latter has very large incisors, the former, small ones with a faint groove near the center, which seems to be a characteristic of *I. typus*. In a young *Aplodontia*, the anterior face of both upper and lower incisors bears a considerable number of longitudinal grooves, as in *Castoroides*. In an adult sewellel, however, there seems to be no trace of such grooving, the incisors being perfectly smooth. This is undoubtedly an age character. The lower incisors of *Ischyromys* are fairly uniform in pattern, having a straight front for the median half of each tooth, and then curving rapidly around laterally. The enamel is continued well onto the sides of the tooth. The upper incisors, on the contrary, have a more uniformly curved anterior face. This is equally true of *Aplodontia*.

Ischyromys has the dental formula of $P\frac{2}{1}$, $M\frac{3}{3}$. $P\underline{3}$ is a very small tooth; usually, however, not a simple cone, but with a greater or lesser development of peripheral cingula, which may extend all around the tooth, or which may be limited to the anterior and posterior sides, or even to the posterior side alone.

$P\underline{4}$ is generally not molariform, but approaches that condition. The hypocone varies from weak to absent. Usually the valley between it and the protocone does not appear as a groove (hypostria) on the lingual surface of the crown, a distinction from the molars. The large paracone and metacone are connected by transverse crests with the protocone and hypocone (when present), respectively. There is no trace of either of the conules. Anterior and posterior cingula are present, the former ending laterally in a small parastyle, the latter connecting with the lingual side of the metacone. There is a small mesostyle.

The first two molars differ from the premolar chiefly in being definitely quadritubercular, with the hypocone quite distinct. These two teeth are quadrate in outline, the others more rounded.

The anterior half of $M\underline{3}$ resembles that of the other molars. The hypocone is poorly developed. The metacone is far to the rear. The metaloph, instead of being straight, as are all the other lophs of the entire cheek tooth series, is curved, the convex side being forward. The posterior cingulum is likewise curved, but in the opposite direction. The

metaloph is of about the same length as in the other molars, but since it is curved, the transverse diameter of this half of the tooth is less than in the other molars.

The lower teeth are all of nearly the same pattern. The only exception is the trigonid of $P\overline{4}$, which consists of two cusps with no continuous anterior cingulum. There is a short crest from the protoconid, however, which runs forward and down the face of the tooth. A well developed hypolophulid I is present as well as a strong posterior cingulum. The hypoconulid is weak (Figs. 21 and 23).

In the molars, the protoconid and metaconid are connected by a metalophulid II. The anterior cingulum is as short as the posterior cingulum of the upper teeth. The ectolophid is present but not accentuated. There is no mesoconid.

The lower teeth are much more nearly bilobate than are the uppers, the trigonid and talonid each forming a high anticlinorium, each with its smaller divisions. Upon wear, the tooth appears definitely bilobate.

Friant (1935) has recently figured unworn teeth of *Ischyromys*, commenting on their supposed similarity to those of Theridomyids. The similarity, of course, is only that of any fairly primitive rodent to a specialized form. She disagrees with the derivation of rodent cheek teeth from tuberculo-sectorial ancestors, but does not specify from what source they have been derived. In this she is approaching more closely to my own point of view. There is no doubt that the rodents cannot be proved to have been derived from tuberculo-sectorial ancestors. The earliest known rodents have a tooth pattern far from tuberculo-sectorial, and it cannot be proved that all later rodents are derived from *Paramys*-like forms. So that for the present we must limit ourselves to stating that the rodent tooth patterns seem to have been derived from an ancestral pattern something like that of *Paramys*, and that the pattern of the Lower Eocene forms generally referred to *Paramys* could, without too great a stretch of the imagination, be derived from the tuberculo-sectorial type. Moreover, there is no evidence to support a belief that rodent dental evolution has involved progressive simplification, but a great deal of evidence to the contrary. So that, while the source of the rodent tooth pattern cannot yet be proved, the tuberculo-sectorial type seems intrinsically far and away the most likely.

One common variation in the teeth of *Ischyromys* is the presence of a crest damming the median valley between the paracone and metacone or between the metaconid and entoconid. Whether this is a specific character or an individual variation, I do not know. It does not characterize any of the species that are here recognized. Only one such specimen has been figured, by Leidy (1869, Pl. 26, Fig. 5).

$DP\underline{3}$ agrees with $P\underline{3}$ in being a small tooth, quite simple and essentially an unmodified cone. $DP\underline{4}$ is rather different from $P\underline{4}$, and less molariform. The anterior cingulum is large. The parastyle is sometimes connected with the paracone, sometimes with the protocone. The paracone may unite with the metacone and the protocone with the hypocone, surrounding a central basin. The hypocone is strong, being as large as in any of the molars. The metacone is small, and the posterior cingulum is short and free.

$DP\overline{4}$ differs from $P\overline{4}$ in the absence of a continuous ectolophid and the independence of the two anterior cusps. The trigonid is usually narrower than in the molars.

Comparisons have been made between the skeleton of *Ischyromys* and that of four other forms. *Paramys* has been selected as representing as closely as we can come at the

present time to the ancestral rodent skeleton. Entirely aside from its relationships, if any, to later forms, *Paramys* is probably relatively primitive, particularly in the skeleton. *Aplodontia* has been selected as being the form which seems to agree most closely with *Ischyromys* in skeletal characters, even though they belong to distinct superfamilies. *Sciurus* represents one of the more primitive of recent rodents. *Cynomys* has been included in the comparisons because Troxell (1922) considered that *Ischyromys* was a possible ancestor of the prairie dog. A few comparisons have been made in particular cases with members of the "Hystricomorpha" that show resemblances to *Ischyromys*.

The only authors that have described any portions of the post-cranial skeleton of *Ischyromys* are Cope (1884) and Troxell (1922). Troxell compared the skeleton with that of *Cynomys*, and considered that the similarities were so great that the two forms must have been closely related. As I shall indicate below, the similarity does not seem to me to be as close as it did to Troxell.

Of the material figured by Cope (1884, Pl. LXVII, Figs. 7–12), one of the distal portions of the humerus (loc. cit., Figs. 8, 8*a*, and 8*b*, Amer. Mus. No. 5412) belongs to *Ischyromys*. The perforation of the super-trochlear fossa in this specimen is apparently an artifact. The other distal end of a humerus (loc. cit., Fig. 7, Amer. Mus. No. 5411), which is much more slender, as well as smaller, with smaller entepicondyle, smaller supinator crest and larger olecranon fossa, belongs to a rabbit. Two astragali (Amer. Mus. Nos. 5415 and 5420) are figured (loc. cit., Figs. 11, 11*a* and 11*b*), which are similar to the astragalus of *Ischyromys*, but are smaller than those described below, and have distinctly longer tibial keels. They probably, however, belong to *Ischyromys*, though quite possibly not to *I. typus*. The pelvis (loc. cit., Figs. 9, 9*a*; Amer. Mus. No. 5413) is also that of *Palaeolagus*. The calcaneum (loc. cit., Figs. 12, 12*a*; Amer. Mus. No. 5416) is that of *Ischyromys*. The tibia (loc. cit., Figs. 10, 10*a* and 10*b*; Amer. Mus. No. 5414) does not seem to belong to *Ischyromys*, but its generic allocation is uncertain.

During the course of this study, I had the good fortune to come across two extremely good skeletons of *Ischyromys* in the American Museum collections, Nos. 1414 and 12,247, from the Middle Oligocene of South Dakota. These were augmented by a partial skeleton of *I. parvidens* from South Dakota, Amer. Mus. No. 12,249. A partial pes from Pipestone Springs, Amer. Mus. No. 9721, helped to fill in blanks. These specimens cover all the skeleton except the manus, part of the pes, and the distal portion of the tail.

It is impossible to work out the *vertebral formula* with exactitude from any of the material now available. There were, of course, seven cervicals. The number of thoracics is uncertain, the largest number preserved on any one specimen being six. There were apparently, however, twelve in all. There were seven lumbars. There was apparently one sacral and two pseudosacrals, and an unknown number of caudals. Amer. Mus. No. 1414 possesses ten caudals, which seem to begin with the beginning of the series, and obviously end far short of the end of the tail, the last bone preserved still being large and massive. By comparison with *Sciurus*, *Paramys*, and other long-tailed forms, it is estimated that there were between twenty-five and thirty bones in the tail.

The vertebral formulae of *Ischyromys*, *Aplodontia*, *Cynomys*, *Sciurus* and *Paramys* are as follows:

	Ischyromys	*Aplodontia*	*Cynomys*	*Sciurus*	*Paramys*
Cervicals	7	7	7	7	7
Thoracics	12	13	12	12	12
Lumbars	7	6	7	7	7
Sacrals	1	2	2	1?	1
Pseudosacrals	2	3	2	2?	2
Caudals	10+ (estimated at 25–30)	9	9+	28	26+ (estimated at 29)

The *cervical vertebrae* are much longer than in either the sewellel or the prairie dog, giving the animal a definitely long neck, clearly separate from the body. The atlas is much heavier than in *Aplodontia* and *Cynomys*, but is close to the former in its configuration. The transverse processes are very large, being extended toward the posterior side of the bone. The vertebrarterial foramen and atlanteal foramen are both large, as in *Aplodontia*, instead of being quite small as in *Cynomys*. There is, however, no trace of the deep groove running forward from the atlanteal foramen to the neural canal, which is present in *Aplodontia*. There is a short spine, which is entirely absent in both of the recent genera.

The *axis* is broad and heavy, with a large massive spine, closely agreeing with *Cynomys*, and quite different from the relatively small bone with a long slender spine found in *Aplodontia*. The centrum is long, antero-posteriorly, as in the prairie dog, while it is short in the sewellel.

The axis and posterior cervicals possess heavy ventral keels, which are entirely absent in both *Cynomys* and *Aplodontia*. The cervicals are much heavier than those of either of these genera, but are nearer the former in this respect. The neural arches are flatter than in either recent genus. In dorsal view, the arches are straight, as in *Aplodontia*, rather than being chevron-shaped, with the point directed anterad, as in *Cynomys*. The ventral portion of the transverse process of the sixth cervical is much larger than in either of the recent forms. This process, however, agrees with that of *Aplodontia* in extending only to the rear, instead of both forward and backward, as in all other rodents with which I am familiar. The cervical spines are short in all forms compared.

The *thoracic vertebrae* agree closely with those of *Aplodontia*, showing no significant differences. As in *Aplodontia*, the spines of the postaxial cervicals are very short, while those of the first two thoracics are long, tapering rapidly behind these bones, so that by T-4 the spines again become extremely short. The presence of an extra rib in *Aplodontia* as compared with *Ischyromys* and *Cynomys* is probably of little significance, these last, as may be seen by their agreement with *Paramys*, being the more primitive in this respect.

The transverse processes of the *lumbars* are like those of *Aplodontia* rather than those of *Cynomys*. The spines of the last lumbars are very high, being even higher than in *Cynomys*, and much higher than in *Aplodontia*. There is a strong ventral keel on the posterior lumbars, very much like the keel on the anterior dorsals. The intervening members of the series have smooth ventral surfaces.

There is one *sacral* and two *pseudosacrals*, one less of each than in *Aplodontia* and *Cynomys*, but agreeing with *Paramys*. The ilio-sacral articulation is quite different in

shape in the various forms, being about the same height in *Ischyromys* as in *Aplodontia*, but much longer in the latter. The transverse process of the bone is much longer in *Ischyromys*, so that the ilium is held at a considerable distance from the mid-line, in contrast to *Aplodontia*, where the extremely short transverse processes bring the pelvis very near the center of the body. The conditions in the sacrum seem much like those in *Paramys*. The angle between the sacrum and the pelvis is slight, as in *Paramys* and *Sciurus*.

The short tails of *Aplodontia* and *Cynomys* are burrowing adaptations. The long tail of *Ischyromys* signifies an absence of such an adaptation, and suggests the possibility of an arboreal heritage. Many forms of murids with a completely terrestrial habitus, however, have as long and as large a tail as that of *Ischyromys*. The centra of the caudals preserved in Amer. Mus. No. 1414 increase in length from 8.5 mm. for the anterior one to 12.4 for the posterior. The diameter of the articular surface of the centra of these bones is essentially uniform. This indicates that the tail must have tapered extremely gently, and hence must have been quite long. The longest caudal was probably the tenth, eleventh or twelfth. In a skeleton of *Sciurus*, the first caudal is 4.7 mm. long, and the tenth 10.7, and increase of over 100 per cent in length, instead of less than 50 per cent as in *Ischyromys*. This suggests a heavier and perhaps a longer tail than in either *Paramys* or *Sciurus*. The neural arch was continuous as far as the tenth caudal, but it seems likely that it was interrupted on the eleventh. This is one later than in *Sciurus*. The caudal vertebrae have two ridges on either side of the midline on the ventral surface of both anterior and posterior ends, probably marking the position of the chevrons, in which case these last must have been unusually large.

A number of *rib* fragments are preserved. The most striking feature of these is the marked angle just ventrad of the tubercle. Hence, although the ribs leave the vertebral column almost horizontally, they quickly turn and hang almost straight down. This results in quite a narrow chest, as contrasted with the very broad one of *Aplodontia*.

The *scapula* (Pl. XXV, Figs. 1, 1*a*) is not well preserved in any specimen of *Ischyromys* that I have seen. The glenoid fossa and the coracoid are very like those of *Paramys*, the glenoid being wider than in *Aplodontia* or *Cynomys*, and the coracoid more distinctly set off from the rest of the bone. The metacromion seems to have been small as in *Aplodontia*, rather than large as in *Paramys* or very large as in *Cynomys*. There is no suggestion that the supraspinous fossa was anywhere near as large as in *Cynomys* and *Paramys*, apparently more nearly resembling *Aplodontia* in this character.

The *clavicle* is present in Amer. Mus. No. 1414. This bone varies considerably as to curvature, among different specimens of *Aplodontia*. It seems, however, to have the same sigmoidal curves that are present in the bone in *Ischyromys*. In *Cynomys* the bone is much straighter, and in both genera it is straighter and much heavier than in *Ischyromys*, in which form it is quite slender, with very well marked curves. These curves in *Ischyromys* necessitate the forward displacement of the lower end of the scapula, which has to lie well forward of the anterior end of the sternum.

The *humerus* (Pl. XXV, Figs. 3, 3*a* and Troxell, 1922, Fig. 7A) differs in detail from that of both *Sciurus* and *Paramys*, though all three forms are similar in its main outlines. The humerus of *Aplodontia*, however, is almost the exact counterpart of that of *Ischyromys*. The bone is somewhat more slender in *Ischyromys* than in *Aplodontia*, thus suggesting *Cynomys*. The tuberosities are larger in *Aplodontia* than in *Ischyromys*, the latter agreeing

with *Paramys* in this character. The greater tuberosity extends more mesiad in *Ischyromys* than in either *Paramys* or *Sciurus*, crowding the bicipital groove. The deltoid process is proximad of the middle of the shaft in all the forms. Compared with *Aplodontia*, the process is nearly the same, that of the fossil not rising quite so sharply from the shaft. The process is bent even more laterad in *Ischyromys* than in *Aplodontia*, though it is by no means as much so as in *Palaeocastor*. The deltoid crest ends in a discrete swelling in *Ischyromys* and *Aplodontia*, whereas in *Cynomys* and *Sciurus* there is a continuous crest. Proximad of the process is a large flat area of muscle attachment, continuing the deltoid process as a surface rather than as a ridge as in *Paramys* and *Sciurus*. This broad, flat area is more like *Cynomys* than like *Aplodontia*. The supinator crests are similar in all of these genera. There is a continuous ridge from the deltoid to the entepicondyle, differing from both *Paramys* and *Sciurus*. There is a distinct supratrochlear fossa in *Ischyromys*, in this resembling *Sciurus* and differing from *Paramys*. The trochlea and capitulum reach much more nearly the same level than in either *Paramys* or *Sciurus*, where the former extends definitely distad of the latter. The distal end is extremely similar in *Ischyromys* and *Aplodontia*, the only appreciable differences being the more bulbous capitulum of the former, in which it agrees with *Paramys*. On the posterior side, the identity is equally marked, both *Aplodontia* and *Ischyromys* showing a small medial process, half way between the level of the deltoid and the head, not visible in either *Paramys* or *Cynomys*. From this view, the head appears distinctly more pendulous in *Ischyromys* than in *Paramys*, though less so than in *Sciurus*. The supinator crest, when seen from this point of view, is not quite as large as in *Sciurus*, and is more flaring than in *Paramys*. The trochleae and olecranon fossa seem very similar in all three. There is no similarity at all between the humerus of *Ischyromys* and that of heteromyids (Wood, 1935, Figs. 57 and 121; 1936*c*, Fig. 6). All the "Hystricomorphs" differ from *Ischyromys* in having lost the entepicondylar foramen, and most of them have a supracondylar fenestra. While both of these are progressive characters among the recent forms, the construction of the rest of the humerus is not as close to that of *Ischyromys* as is even the humerus of *Sciurus*.

Among the material from Pipestone Springs, referred to *I. pliacus*, is the distal end of a humerus, which shows no differences from that of the forms from the Oreodon Beds, except that it seems somewhat smaller.

The comparison of the *radius* and *ulna* with the corresponding bones of *Aplodontia* is a little difficult, the only specimen of the latter available to me and containing these bones being a juvenile. I have therefore made use of quotations from Coues (1877) to show how closely these bones agree in *Ischyromys* and *Aplodontia*.

The head of the *radius* is much elongate transversely, the long diameter being about twice the short, thus differing from *Paramys*, *Cynomys* and *Sciurus*, where the long is about one and a half times the short. *Aplodontia* approaches *Ischyromys* in this condition. The head is of uniform width, instead of narrowing laterally as in the other genera. The tuberosity is larger than in *Paramys*, but smaller than in *Sciurus*. The radius has very little trace of the sigmoidal curve seen in this bone in *Paramys*, but is arched in the same manner, thus differing from *Sciurus* and *Cynomys*, where it is more nearly straight. The distal third of the ulna and half of the radius are marked by very deep fossae which fit into each other quite closely. The proximal parts of the bones are rather widely separated. Coues (1877, pp. 579–580) describes the radius of *Aplodontia* as follows: "The radius . . .

lies close to the ulna its whole length; the shaft is much bent outward; the head is oval in section. . . . Notwithstanding the restriction of motion which the close apposition of the ulna and radius would indicate, the relations of their various articular surfaces are the same as those in cases where pronation and supination are perfect, and such movements are doubtless considerable in extent." Rotation of the hand in *Ischyromys* must, however, have been limited, the distal ends of the radius and ulna being so closely appressed as effectually to prevent supination and pronation, thus being radically different from *Paramys*, *Sciurus* and *Cynomys*, and agreeing closely with Coues' comments on *Aplodontia*. This restriction of movement seems to have been present in spite of the large size of the supinator crest of the humerus.

The olecranon has a much greater mesiad curve than in *Paramys*, and a greater one than in *Sciurus*. The shaft curves laterally, instead of being straight as in the other two forms. There is a very deep fossa running the entire length of the mesial surface of the bone, only faintly indicated in *Paramys*, and not at all in *Sciurus*. It is bounded laterally by a crest, which runs half the length of the bone, from the coronoid process distally. The distal portion of the fossa is deepened to serve for articulation with the radius. This portion is bounded laterally by a very high, narrow crest. In describing the ulna of the sewellel, Coues says (1877, p. 579) that the "inner face of the shaft is deeply grooved for the reception of the radius, which lies in close apposition with the ulna for the whole of its own length; but the ulnar groove continues up beyond the head of the radius. On the inner face of the bone, a somewhat similar groove runs from the side of the olecranon past the joint, but soon becomes obsolete. The ulna ends below with a simple conical extremity, which takes but little share in the formation of the wrist joint." The distal end of the ulna of *Ischyromys* is almost exactly the same as that of *Aplodontia*. There is another fossa at the proximal end of the lateral surface, beginning at the end of the olecranon and running a third of the length of the shaft. A similar fossa occurs in *Palaeocastor*. This and the uniform curve of the radius are the only similarities in the fore arm between that form and *Ischyromys*. No trace of this proximal fossa occurs in either *Paramys* or *Sciurus*.

The *manus* is practically unknown. Two or three phalanges which probably belong to the manus are associated with the American Museum skeletons. As there is no certainty which belong to the manus and which to the pes, or to which digit they belong, it is not considered worth while describing them.

The *pelvis* is quite different from everything with which I have compared it, differing from many of the forms in almost every possible manner. This is especially clear of the ilium (Pl. XXIII, Fig. 7), where the gluteal fossa is very large, and nearly vertical, instead of being nearly horizontal as in *Aplodontia*. In a young *Aplodontia*, however, the fossa approaches more nearly to the position seen in *Ischyromys*. I know nothing, however, really close, though there are certain similarities to the erethizontids. The gluteal fossa begins about half way between the acetabulum and the anterior end of the bone, the iliac border flaring rapidly outward and, especially, upward. The acetabular border forms a heavy crest almost at the ventral surface of the bone, thus differing from all forms that have been compared, where the crest lies more nearly in the middle of the bone. The ilium is not everted as much as in *Cynomys*, being nearer to *Aplodontia* in this respect. It is, however, quite different from the ilium of *Paramys*, which is rod-like, and almost an equilateral triangle in cross section. The gluteal fossa in the Bridger form is distinctly

smaller than the iliac fossa. The ilium is also proportionately much shorter than in *Ischyromys*. The knob anterior to the acetabulum is rounder than in either *Sciurus* or *Paramys*, where it is elongate, while it is absent in *Aplodontia*. There is a trace of the pectineal tubercle on the anterior margin of the pubis, slightly posterad of this knob. The pubis slopes rapidly caudad, the anterior end of the symphysis being behind the acetabulum. The symphysis, however, is as long as in *Cynomys*, not having suffered the extreme reduction seen in *Aplodontia*. The pubis has a straight or slightly concave anterior face. The bone is heavier than in *Aplodontia*. The long diameter of the obturator foramen runs from the acetabulum to the posterior end of the symphysis, and approaches that of *Cynomys* in shape. The ischium is broad and flat, and, posteriorly, quite thin. It is more like that of *Cynomys* than that of *Aplodontia*, and rather like that of *Paramys*. In short, the pelvis combines features of *Cynomys*, mostly not seen in *Aplodontia*, with a number of features which I have not been able to find duplicated elsewhere among the rodents. In general appearance, though not in the details of construction, there is considerable similarity to the pelvis of *Erethizon*, which may mean a similarity of habitus.

The *femur* is much shorter in proportion to the humerus than in *Paramys*, and slightly more so than in *Sciurus*, the measurements of the humerus being 80.6, 68.4 and 78.8 per cent respectively of those of the femur. In other features, the bone is closer to that of *Paramys* than to that of the squirrel. As will be shown below, it is very similar to the femur of *Erethizon* and *Aplodontia*. The head is lower than the great trochanter, as in *Sciurus* and *Paramys*. The neck is longer than in either of these forms. The length of the neck shows up clearly in posterior view (Pl. XXV, Fig. 6*a*). The head is on the proximal end of the bone, rather than at right angles to the neck. This means that, if the pelvis were vertical, the femur would be at an angle of about 45° with the vertical. In *Paramys*, the femur would be only 30° from the vertical, in *Sciurus* not over 25° or 30°. In *Aplodontia*, the femur is at an angle similar to that in *Ischyromys*, and greater than that in *Cynomys*. The neck, in *Aplodontia*, is much shorter than in *Ischyromys*. The trochanteric fossa is deeper than in *Paramys*, resembling *Sciurus* in this respect. As in *Paramys*, the crests from the greater and lesser trochanters extend distad and meet. This union is more marked, however, than in *Paramys*. There is no trace of the broad, flat area observable here in *Sciurus*. The lesser trochanter is on the posterior surface of the bone as in *Paramys* rather than the mesial as in *Sciurus*. The trochanters resemble those of *Aplodontia*, the lesser being small, and hardly visible in the anterior view of the bone. The third trochanter is even lower on the bone than in *Paramys*, being at nearly the middle of the shaft, rather than high as in sciurids and heteromyids. The trochanter ends in a knob, recurved posterad. The size and position of the third trochanter makes the whole shaft seem broad and flat (Pl. XXV, Figs. 6 and 6*a* and Troxell, 1922, Fig. 7B). Hence, the shaft does not thin as in *Sciurus*, but retains the same width throughout. The third trochanter is even lower on the shaft than in *Aplodontia*, but is much more like that form than like *Cynomys*, and, as in *Aplodontia*, it is long and low, extending along a considerable portion of the shaft. The shaft is much more robust than in *Cynomys*, as in *Aplodontia*, but even more so. It closely resembles that of *Erethizon*. The shape of the third trochanter is very suggestive of that of *Palaeocastor* (Peterson, 1906, Pl. 18, Fig. 12). The femur is not at all like that of the mylagaulids, where the third trochanter is high on the bone, more like the squirrels, and is quite different in shape from that of *Ischyromys*.

In the form of the patellar groove, *Ischyromys* differs from both *Paramys* and *Sciurus*, the groove being narrow and running somewhat laterad toward its proximal end. The shape of the intertrochlear fossa is different from that of the other two genera, being deep and narrow. The medial trochlea is distinctly the larger, being even larger than in *Paramys*. It extends quite far posterad, much further than in the Bridger form. No such enlargement of the trochlea exists in *Sciurus*.

Amer. Mus. No. 9721, an *Ischyromys* cf. *pliacus* from Pipestone Springs, contains the middle of a femur including the third trochanter. This differs from Oreodon Beds femora in the distinctly smaller size of the third trochanter. This does not seem to be an age character, the animal appearing fully adult, but seems rather to represent a more primitive stage in ischyromyid evolution.

The *patella* is long, narrow and thick, being nearer to that of *Aplodontia* than to that of *Cynomys*, but not close to either.

The *tibia* combines features of *Erethizon*, *Aplodontia* and *Cynomys*. The cnemial crest extends far down the bone as in *Erethizon*. There is no evidence of the sigmoidal curve which occurs in *Aplodontia*. The shape of the posterior surface, however, is much like that of *Aplodontia* and *Paramys*. The tibia and fibula were separate throughout as in the last two genera, though they were closely united, and apparently immovably attached to each other, distally, by connective tissue. The lower end is similar to that of *Cynomys*, and quite different from that of *Paramys*. No *Aplodontia* material is available for comparison of the distal portions.

Unfortunately, all of the skeletons included in this study have their tibias badly damaged. An isolated tibia (Amer. Mus. No. 9659) from Pipestone Springs, however, shows the same marked curvature near its center that Troxell indicated for this bone (Troxell, 1922, Fig. 7*c*), and the figure in Pl. XXVI is based on this specimen.

Both ends of the fibula are preserved. The distal end is similar to that of *Cynomys*, but much heavier. It is three-pointed when viewed from below, with a strong external malleolus not seen in *Paramys* but present in *Cynomys*. The proximal end is long and slender in proximal view, more so than in *Cynomys*, *Aplodontia* or *Paramys*, and the shaft is attached at one extremity of the head.

The *pes* shows an extreme condition of lengthening of the astragalus, which reaches the middle of the cuboid. I have seen no other rodents in which this occurs, though *Palaeocastor* approaches it and the astragalus of *Mylagaulus* reaches about a third of the way down the cuboid. In *Aplodontia* (Tullberg, Pl. 34, Fig. 23), the astragalus and calcaneum reach the same level. Essentially the same is true of sciurids. Not enough is known of the foot to determine its general proportions.

The *astragalus* is long and slender as in *Sciurus* rather than short and broad as in *Paramys*. Otherwise, it is much more like the latter, except in the very short tibial trochlea, which is again like *Sciurus*. The head is rounded as in *Paramys*, instead of flattened as in *Sciurus*. The medial margin is continuous with the tibial trochlea as in *Sciurus* rather than forming a broad medial shelf as in *Paramys*. The surface of the trochleae resembles *Paramys* in being smooth, rather than with a distinct tibial fossa, as in *Sciurus*. The shape of the ectal and ental facets is very much like that of the same surfaces in *Paramys*, the only differences being correlated with the longer neck of *Ischyromys*. There are variations in size among astragali referable to *Ischyromys*, but whether the variation is specific or

individual cannot be told at the present time. Probably both types occur. There appear to be slight differences in detail between astragali from Pipestone Springs (Amer. Mus. No. 9721) and those from the Oreodon Beds. The rounded head of the astragalus is strikingly different from the flat end found in *Mylagaulus*.

The *calcaneum* is widely expanded distally, there being a broad process on both medial and lateral sides. The anterior view of the distal end of the bone is quite characteristic, bearing an oval facet with its long axis vertical (Pl. XXVII, Fig. 3). This and the broad lateral processes are quite diagnostic, not occurring in any other Oligocene rodent, as far as I am aware, except *Titanotheriomys*. The lateral processes are quite like those of *Mylagaulus*, to which this calcaneum is fairly similar. The calcaneum of *Aplodontia* is likewise apparently similar, Coues stating that "the anterior extremity is somewhat three-pronged, the inner anterior corner forms a broad shelf . . ." (Coues, 1877, p. 582). The tuber calcis is deep grooved.

The *cuboid* is more constricted in the middle than in either *Paramys* or *Sciurus*, being of a distinctly hour-glass shape. The *Mylagaulus* cuboid is straight, or even convex, sided, in dorsal aspect. There is a broad medial facet with which the lateral part of the head of the astragalus articulates. The distal face of the cuboid comes about the middle of the navicular. There is a distinct angle between the cuboid and metatarsal IV, the latter sloping upward, giving the foot a distinct arch.

The *navicular* is quite narrow dorsally, but widens considerably toward the plantar surface. The proximal end is concave for the round head of the astragalus. The distal end is divided into two clear facets by a strong vertical ridge in its center. As in *Paramys*, the facet for the entocuneiform is entirely on the mesial surface of the bone.

The rest of the pes is known only from various fragments which have not been identified with certainty.

A study of the limb ratios unfortunately does not reveal as much as might be hoped as to the habits of *Ischyromys*. That is, the limbs approach the equality in length found

	Ischyromys	*Aplodontia*	*Cynomys*	*Sciurus*	*Paramys*	*Perognathus*
R + H	81.1	ca. 67	83.8			17.50
F + T	ca. 106	ca. 89	103.7			22.35
Intermembral Index	78.6	75.3	80.8	68.5	68.4	78.0

in *Cynomys*, and the fore limb is longer proportionately than in *Aplodontia*, both of which are burrowing forms. The similar limb ratio occurring in *Perognathus flavus flavus* (Wood, 1935*a*, Table V) was interpreted by Wood as a scampering ratio. This suggests that there is no necessary change in limb proportions in changing from a scampering to a fossorial habitus, which would, therefore, be the easiest change in habitus for an animal to make. It seems probable that *Ischyromys* was making this change, the absence of fossorial adaptations in the skull and the long tail merely indicating that the transition was still in progress, and not yet complete.

As can be seen from the above description, the skeleton of *Ischyromys* shows numerous close similarities to that of *Aplodontia*, which strongly suggests that the zygomasseteric resemblances of the two families are, in this case at least, a correct indication of their

relationships. There are certain real similarities to *Paramys*, suggesting that that form has been correctly considered one of the most primitive of the rodents. There are also respects in which *Ischyromys* agrees with *Sciurus, Marmota, Cynomys, Hystrix, Atherura, Coendu* and *Erethizon*. The South American tree porcupines agree very closely with *Ischyromys* in the characters of the femur, having the same shaped head, neck, shaft and distal end. In some of them the third trochanter is even further distad than in *Ischyromys*. The hystricids agree in some points, but are not as close as are the erethizontids. In the cursorial South American forms, the limbs have become elongate, and the resemblances to *Ischyromys* are much less. The erethizontids agree in shape of the femur even more closely with *Ischyromys* than does *Aplodontia*. Whether or not this is indicative of a real relationship must be left for future work to decide, being entirely beyond the scope of the present study. It seems certain that there is no relationship between *Ischyromys* and any of the "Sciuromorphs."

The skeleton of *Ischyromys* is sufficiently like that of *Aplodontia* to warrant our assuming not only that there was a close affinity between the two genera, but also that the habitus and mode of locomotion in the two cases were essentially similar, though, as is indicated by skeletal similarities to *Paramys, Ischyromys* was distinctly more primitive than is *Aplodontia*. This suggests that the fossil was a burrowing form, with a slow, ambling gait, which escaped his enemies by spending much of the time in burrows in the ground. As far as I am aware, *Ischyromys* remains are found only in flood-plain deposits, never in the channel sands. Matthew (1901, p. 369) specifically makes the statement that such was the case at that time, and I know of no specimens that go counter to the general rule. It is probable that *Ischyromys* was more like the marmots or the prairie-dogs than like the sewellel in his habits. He quite likely made burrows and lived in them, but did more of his foraging above ground. The long tail suggests that he had had a short pre-Oligocene burrowing ancestry, so that his heritage was that of a terrestrial or arboreal form, even though his habitus was being established as a fossorial one.

The following summary of the habits and habitat of *Aplodontia* would probably apply equally well to *Ischyromys*. "*Aplodontia* is herbivorous, colonial, nocturnal, and fossorial. A considerable degree of humidity and an abundant supply of food plants seem to be necessary conditions to its existence. Situations well sheltered by a tangle of vegetation are usually chosen for its burrows. Its nest is made underground, in an enlarged chamber. . . . Sight and hearing are apparently defective; but smell and touch, particularly the latter, appear to make up for any deficiencies in these respects" (Taylor, 1918, p. 450).

The pre-Oligocene history of the ischyromyids can be sketched only in the most general terms. The most logical assumption at present is that they were derived from the stock of rodents represented by the Bridger sciuravids, as was indicated by Burke (1935*a*). The Uinta genus *Pareumys* apparently represents a stage intermediate between *Ischyromys* and the forms Troxell (1923*b*) included under the genus *Tillomys*. Its exact relationships with either genus, however, are not quite clear at the present time.

After the close of the Oligocene, no ischyromyids are known. Whether the line became extinct, or whether they have a special relationship with the Allomyidae, and hence, presumably, with the mylagaulids and aplodontids, can be determined only after a careful study of the John Day fauna. For the present, at least, the line must be considered as

ending with the close of the White River. This is rendered more probable by the entire dissimilarity between the tooth pattern of *Ischyromys* and that of *Eohaplomys* from the Upper Eocene of California (Stock, 1935, Pl. 6).

As has been suggested above, there are certain points of similarity between *Ischyromys* and various of the "Hystricomorphs," especially the erethizontids. Whether there is any especial significance to this cannot be told without a detailed study of the anatomy of the porcupines, which is not practicable at the present time.

It is impossible to include a satisfactory revision of the species of *Ischyromys* at this point. The material to do this is undoubtedly available, but the time is not. Nor is this the proper place, this account being primarily a review of the genera. It appears that there are at least four species of *Ischyromys:* one small form, *I. parvidens;* two medium sized ones, *I. typus* and *I. troxelli;* and one large one, *I. pliacus*. The material referred to *I. parvidens* seems of fairly uniform quality. That referred to the other three species is extremely variable, and each one may represent several distinct forms.

The only recent attempt to revise the species of the genus was by Miller and Gidley (1920). They recognized *I. typus* and *I. chrysodon*, and erected a new species, *I. parvidens*. The only characters they use to separate *I. chrysodon* from *I. typus* are the presence of a pit in front of the cheek teeth in the former, and of only a shallow depression in the latter. Troxell (1922) described certain new forms, but did not attempt to revise the genus. I have made the primary separation on the basis of size, but have also used the construction of the masseteric plate, the proportions of the teeth, the relative lengths of the brain case and of the orbit, and the skull width at the postorbital constriction as subsidiary specific characters.

Ischyromys typus Leidy 1856

Ischyromys typus Leidy 1856.
Colotaxis cristatus Cope 1873*a*.
Gymnoptychus chrysodon Cope 1873*c*.
Ischyromys chrysodon (Cope), Cope 1873*b*.
Ischyromys typus lloydi Troxell 1922.

(Fig. 21)

Leidy, 1869, Pl. 26, Figs. 3–6; Cope, 1884, Pl. LXVII, Figs. 1–12, Pl. LXVI, Fig. 30; 1888, Fig. 5; and Troxell, 1922, Figs. 4–7.

Holotype: Acad. Nat. Sci. Phila., No. 11,015, a fairly complete skull.

This species is of medium size. The skull is relatively wide at the postorbital constriction, being about ten millimeters across at the narrowest point. The nasals are long, extending two millimeters or more behind the premaxillaries. The interparietal is broadly rounded instead of having a long, slender anterior process as in the other species of the genus (except, perhaps, *I. parvidens*, the skull of which is unknown). This species is rather primitive in the zygomasseteric area, the masseter being confined to a restricted area below and behind the infra-orbital foramen, and being largely limited to the inferior surface of the zygoma. At the median margin of the narrow masseteric plate, and in front of $P\underline{3}$, is a rather deep pit, nearly completely separated from the fossa. There is a faint groove in the slender upper incisors.

$P\underline{4}$ has an incipient hypocone. $M\overline{1}$–$\overline{2}$ are longer than wide by an appreciable amount.

In all the lower teeth, the posterolophid is extremely well developed, reaching the lingual side of the tooth, and uniting, after little wear, with the entoconid. The tooth row is under 15 mm. long (see table of measurements, p. 189).

One of the striking things about this species is its overwhelming preponderance in the collections from the Cedar Creek Beds. Out of thirty-two specimens in the American Museum collections from Colorado, twenty-nine are referable to this species. It is, however, also represented in the Big Badlands, though it seems to be relatively rare there. Leidy's type was from the northern edge of the Big Badlands; the two referred specimens figured by him (1869, Pl. 26, Figs. 5–6) are from farther south in the main part of the "Mauvaises Terres"; and several specimens from this area in the American Museum, Museum of Comparative Zoology and the author's private collection, seem to belong to this form. There are doubtless many others in collections not included in this study. But this species is distinctly less common in the Big Badlands than are either *I. pliacus* or *I. troxelli.*

Range: Middle Oligocene, especially of northeast Colorado and of the Big Badlands of South Dakota.

Ischyromys pliacus Troxell 1922

(Fig. 22; Matthew, 1910, Figs. 16–18 and Troxell, 1922, Fig. 1)

Holotype: Y.P.M. No. 12511, mandible with $P\bar{4}$–$M\bar{3}$ right.

This is the largest described species of the genus. The skull is highly constricted in the postorbital area, the narrowest point measuring only 9 mm. across. The nasals are

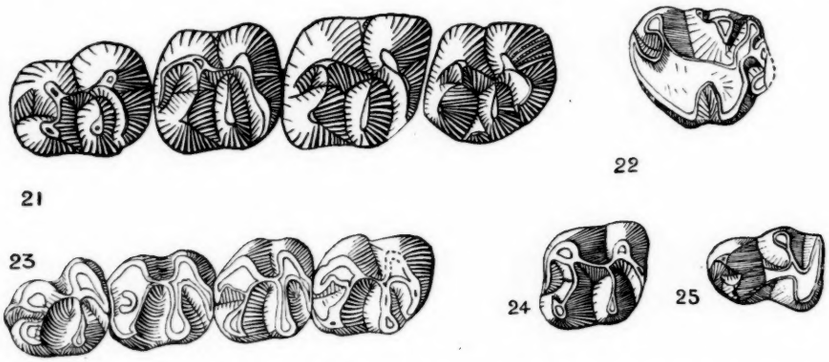


FIG. 21. *Ischyromys typus.* U.S.N.M. composite of two unnumbered specimens.
FIG. 22. *I. pliacus.* Mus. Comp. Zool. No. 17,208. $dP\underline{4}$ right. Anterior end to the right.
FIG. 23. *I. parvidens* Miller and Gidley. Holotype. U.S.N.M. No. 9134, $P\bar{4}$–$M\bar{3}$.
FIG. 24. *I. parvidens.* Can. Nat. Mus. No. 6480, $M\bar{1}$ right.
FIG. 25. *I.* cf. *parvidens.* Mus. Comp. Zool. No. 17,210, $dP\bar{4}$ left.
All figs. × 5.

the same length as the premaxillaries. The interparietal has a long anterior process. The infra-orbital foramen is as in *I. typus.* $P\underline{3}$ is simple, though not an unmodified cone. The hypocone of $P\underline{4}$ is weak. In the lower teeth, the posterolophid is short, not reaching the entoconid. The lower tooth row is over 16 mm. long.

The material referred to this species includes the largest known members of the family. In fact, most of this material is referred to *I. pliacus* simply on the basis of size. Without

MEASUREMENT OF THE HOLOTYPE OF *I. typus*

$P\underline{4}$–$M\underline{3}$	13.67 mm.	$M\underline{2}$ antero-posterior	3.83 mm.
$P\underline{4}$–$M\underline{2}$	10.73	width protoloph	3.50
$P\underline{4}$ antero-posterior	3.50	width metaloph	3.50
width	3.60	$M\underline{3}$ antero-posterior	3.30
$M\underline{1}$ antero-posterior	3.50	width protoloph	3.30
width protoloph	3.80	width metaloph	2.50
width metaloph	3.80		

MEASUREMENTS (IN MM.) OF LOWER TEETH OF *Ischyromys typus*

	A.M. No. 5418	*A.M. No. 5419*	*A.M. No. 5434 juvenile*	*A.M. No. 5439*	*A.M. No. 5442*	*A.M. No. 5444*	*A.M. No. 5447 juvenile*	*A.M. No. 5448*	*A.M. No. 5452*	*A.M. No. 5457*	*A.M. No. 8781*	*A.M. No. 5440*	*A.M. No. 5427*	*A.M. No. 5455*	*A.M. No. 1421*	*A.M. No. 1421*	*A.M. No. 1421*	*A.M. No. 5406*	*A.M. No. 5407*	*A.M. No. 5410*
$P\overline{4}$–$M\overline{3}$, crown													14.8					14.6		
$P\overline{4}$, antero-posterior		4.0				3.6				3.7			3.8					4.0		
$P\overline{4}$, width anterior loph		2.6				2.3				2.9			2.6					2.6		
$P\overline{4}$, width posterior loph		3.1				2.8				3.3			3.2					3.2		
$M\overline{1}$, antero-posterior		3.8			3.6			3.7			3.8	3.6	3.9	3.9	4.1	3.5		3.6	3.3	3.9
$M\overline{1}$, width metalophid		3.25			3.4			3.0			3.0	3.4	3.2	3.3	3.6	3.3		3.3	3.2	2.9
$M\overline{1}$, width hypolophid		3.45			3.7			3.0			3.1	3.4	3.3	3.2	3.6	3.3		3.4	3.5	—
$M\overline{2}$, antero-posterior	3.15		4.00	3.05	3.7		4.2		3.6		3.5	3.7	3.7	3.8	4.0	3.3		3.6	3.8	3.9
$M\overline{2}$, width metalophid	3.7		3.6	—	3.5		3.1		3.4		3.2	3.5	3.3	3.5	3.8	3.5		3.5	3.5	—
$M\overline{2}$, width hypolophid	3.3		3.65	—	3.5		3.7		3.5		3.2	3.5	3.2	3.2	3.6	3.5		3.4	3.4	—
$M\overline{3}$, antero-posterior	4.0			3.9	4.1								4.1		4.0		4.6	3.9		
$M\overline{3}$, width metalophid	3.25			3.0	3.4								3.1		3.6		3.6	3.3		
$M\overline{3}$, width hypolophid	3.0			3.0	3.1								3.0		3.2		3.6	3.1		
$P\overline{4}$–$M\overline{2}$													10.9					10.7		
$M\overline{1}$–$M\overline{2}$					7.0						7.0	7.3	7.4	7.5	7.8	6.6		7.0	6.9	
$M\overline{1}$–$M\overline{3}$					10.9								11.7		11.2			10.7		
$M\overline{2}$–$M\overline{3}$	7.2			7.0	7.8								7.8		7.8			7.4		
depth of ramus at $P\overline{4}$						11.0												10.5		

a careful and detailed revision of the genus, it is impossible to determine which specimens are conspecific with the holotype of *I. pliacus*, and it is likely that several forms are being lumped.

The zygomasseteric area is similar to that of *I. typus*, but the area of origin of the masseter on the zygoma is larger. The pit by the front of the tooth row is broadly continuous with the masseteric fossa. The interparietal is triangular with a long, pointed anterior process. The postorbital constriction is much more marked than in Leidy's form. The orbit, in front of the constriction, is short. The sagittal crest is clearly marked.

P3 is simple, never showing the continuous cingulum seen in *I. typus*. P4 has a poorly developed hypocone, which is sometimes almost entirely absent. The posterolophid of the lower teeth is short, never uniting with the entoconid. The referred mandibles in the American Museum do not show the dental peculiarities of the holotype, which supports the belief that more than one species is included in this material.

Some skeletal fragments from the Big Badlands, in the author's collection, are tentatively referred to this form, even though they are 50 per cent larger than any other ischyromyid bones known.

Most of the material now referred to this species is from the Oreodon Beds of South Dakota. The holotype and Amer. Mus. No. 8726 are from the Cedar Creek; Amer. Mus. No. 9849 is from the Leptauchenia Beds; Amer. Mus. Nos. 9615 and 9648 are from the Pipestone Springs Beds; and Amer. Mus. No. 9721 from the Thompson Creek Beds.

This material seems to represent a line of large forms, ranging throughout the whole of the Oligocene, and, presumably, fairly closely related. Careful study would probably distinguish a number of stages in the various levels of the Oligocene.

MEASUREMENTS OF *Ischyromys pliacus*.

	Amer. Mus. No. 9849	*Amer. Mus. No. 1419*	*Amer. Mus. No. 1421*	*Amer. Mus. No. 1421*	*Amer. Mus. No. 1421*	*A.E.W. No. 2EE2b*	*M.C.Z. No. 17,536*	*M.C.Z. No. 17,536*	*M.C.Z. No. 17,536*
	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
P4–M3, crown	16.0	16.3				16.3	17.0		
P4 a-p	4.1	4.25				4.4	4.1	3.8	
width metalophid	2.7	2.9				3.1	3.1	3.0	
width hypolophid	3.7	3.7				3.6	3.7	3.6	
M1 a-p	3.9	3.8	4.1	4.0	3.7	3.9	3.6	3.6	3.2
width metalophid	3.7	3.8	3.5			3.7		4.0	3.7
width hypolophid	4.1	3.95	3.4		4.0	4.1		4.0	3.7
M2 a-p	4.1	3.8	3.9	4.1	4.0	4.0	4.0	3.8	3.3
width metalophid	3 8	3.75	3.7	4.2	4.1	4.0		4.0	4.0
width hypolophid	4.0	3.75	3.7	3.9	3.95			4.0	
M3 a-p	4.1	3.6				4.3	4.4		4.1
width metalophid	3.5	3.5				3.7	3.7		
width hypolophid	3.3	3.2				3.3	3.5		3.6
P4–M2	12.0	12.25				12.1	12.3	11.9	
M1–M2	7.9	8.2	7.7	8.1	7.8	7.9	8.2	7.7	7.0
M1–M3	11.9	12.0				12.2	12.7		11.3
M2–M3	7.9	8.1				8.3	8.5		7.4
depth ramus at P4	11.9	11.5						11.5	9.7

Range: This species (or group of species) seems to have had a more northern range than did *I. typus*, being the characteristic and abundant *Ischyromys* of the Big Badlands, though it also occurs in the Cedar Creek Beds, in the Leptauchenia Beds of the Big Badlands, and in the Titanotherium Beds of Pipestone Springs and Thompson Creek.

Ischyromys troxelli, sp. nov.[1]

Holotype: Amer. Mus. No. 12,248, fragmentary skull and jaws, Middle Oreodon Beds, W. Sheep Mtn., South Dakota.

This species is of medium size. The zygomasseteric region is suggestive of the "Sciuromorphs," with a broad, gently sloping plate below the infra-orbital foramen, which is, however, free from the masseter, it being limited to an area on the zygoma. The skull width at the postorbital constriction is very small. The interparietal is triangular. $M\bar{1}$–$\bar{2}$ are wider than long. There are short posterolophids on all the lower teeth.

I. troxelli agrees closely with *I. typus* in size, differing, however, in a number of important characters from it. The interparietal is triangular, as in *I. pliacus*. The postorbital constriction is narrow as in that form, being only 8 mm. wide. The orbit, however, is long, being not only relatively, but absolutely, longer than in *I. pliacus*, and much longer than in *I. typus*.

The pit by the anterior end of the upper cheek teeth is very shallow, hardly distinguishable from the broad masseteric plate. This last is much more like that of *Titanotheriomys* than is the case with any other *Ischyromys*, being very broad and uniform, and has begun to impinge on the infra-orbital foramen, the lower border of the foramen being straight instead of rounded as in the other species. The masseter, however, not only did not extend laterad of the infra-orbital foramen, but did not fully occupy this broad plate, the rugosities for the muscle being sharply limited in area (Pl. XXIII, Fig. 3). This is of considerable evolutionary importance, as it represents at least one case where a structure seems to have developed before any associated structure could take advantage of it. That is, the mutation causing the broadening of the plate in this species occurred before the migration of the muscle to occupy the plate. This is, of course, quite to be expected.

The cheek-tooth series are slightly longer than in *I. typus*, averaging slightly over 15 mm. in length. $M\bar{1}$–$\bar{2}$, however, are definitely wider than they are long, in contradistinction to the conditions in *I. typus*. The posterolophid is short on all the teeth, as in *I. pliacus*.

There are several specimens in the American Museum collections which agree with the holotype in all characters except the construction of the zygomasseteric area. Further study would probably warrant their separation, as a distinct species, but for the time being they had best be left with *I. troxelli*.

This species is rarer than either *I. typus* or *I. pliacus*, but still fairly abundant. It seems a typically South Dakota form, only one specimen from Colorado being referred here.

Range: Lower to Middle Oreodon Beds of South Dakota, and Cedar Creek Beds of Colorado.

[1] I take great pleasure in naming this species after Dr. E. L. Troxell. It is appropriate not only because he is one of the few men who have ever done any work on *Ischyromys*, but also, and more particularly, because he was a pioneer in the study of fossil rodents in North America, and is one of the extremely small number of workers who have considered it necessary to base their descriptions of fossil rodents on a study of the specimens themselves instead of illustrations.

MEASUREMENTS OF *Ischyromys troxelli*

	Amer. Mus. No. 12,248 left. Holotype	*Amer. Mus. No. 12,248 right. Holotype*	*Amer. Mus. No. 1426 left*	*Amer. Mus. No. 1426 right*	*Amer. Mus. no No.*	*Amer. Mus. no No.*
	mm.	mm.	mm.	mm.	mm.	mm.
$P\bar{4}$–$M\bar{3}$	15.0	15.3	15.0	—	—	—
$P\bar{4}$ antero-posterior	3.7	—	3.1	3.2	3.5	3.6
width metalophid	—	—	2.7	2.9	3.0	2.6
width hypolophid	—	3.7	3.6	3.8	3.5	2.9
$M\bar{1}$ antero-posterior	3.3	3.3	3.2	3.2	3.2	—
width metalophid	3.7	3.7	3.7	3.7	3.5	—
width hypolophid	4.0	—	3.8	—	3.8	—
$M\bar{2}$ antero-posterior	3.3	3.6	3.8	3.7	3.5	—
width metalophid	4.0	—	3.9	4.0	3.7	—
width hypolophid	3.9	—	3.8	4.0	3.8	—
$M\bar{3}$ antero-posterior	3.6	3.7	3.6	—	—	—
width metalophid	3.4	3.3	3.6	—	—	—
width hypolophid	3.2	3.1	3.2	—	—	—
$P\bar{4}$–$M\bar{2}$	11.2	—	10.6	11.3	11.0	—
$M\bar{1}$–$M\bar{2}$	7.5	7.3	7.7	7.1	6.9	—
$M\bar{1}$–$M\bar{3}$	10.95	11.0	11.1	—	—	—
$M\bar{2}$–$M\bar{3}$	7.4	7.2	7.5	—	—	—
Depth of jaw at $P\bar{4}$	10.7	—	11.3	—	—	—

Ischyromys parvidens Miller and Gidley 1920

(Figs. 23–25; Lambe, 1908, Pl. 8, Fig. 18; Troxell, Figs. 2–3)

Ischyromys parvidens Miller and Gidley 1920.

Ischyromys typus Lambe 1908.

Ischyromys typus nanus Troxell 1922.

Holotype: U.S.N.M. No. 9134.

This species is known at present from lower jaws and from a fragmentary skeleton, Amer. Mus. No. 12,249. The holotype is from the Oreodon Beds of Washington County, South Dakota. The skeleton is from the Lower Oreodon Beds, Quinn Draw, South Dakota.

There seems to be little which distinguishes this species other than its small size, it being much smaller than any other member of the genus. At the same time, as far as the teeth go, it seems somewhat more primitive than do the others. The skeleton seems identical in proportions and in characters with that of the larger forms. The holotype has three mental foramina, which probably is of little or no significance.

The specimen that Lambe described from the Cypress Hills (Fig. 24), and which he referred to *I. typus*, seems to be indistinguishable from the holotype of *I. parvidens*. This group of specimens may represent a line of small species just as *I. pliacus* seems to represent a line of large ones, but there is at present no evidence that more than one form is

involved. The occurrence of this form in the Cypress Hills may merely indicate that Lambe was correct in supposing that he was dealing with a mixed fauna, or it may show this species to be long-lived.

MEASUREMENTS OF *Ischyromys parvidens*

	Holotype, U.S.N.M. No. 9134		*Holotype, U.S.N.M. No. 9134*
$P\underline{4}$–$M\underline{3}$	12.16 mm.	$M\underline{2}$ antero-posterior	2.77 mm.
$P\underline{4}$ antero-posterior	2.97	width metalophid	2.91
width metalophid	2.15	width hypolophid	2.75
width hypolophid	2.70	$M\underline{3}$ antero-posterior	3.38
$M\underline{1}$ antero-posterior	2.97	width metalophid	2.81
width metalophid	2.64	width hypolophid	2.63
width hypolophid	2.62		

Range: Oreodon Beds of South Dakota and Colorado and Lower Oligocene of Cypress Hills, Saskatchewan.

Titanotheriomys Matthew 1910

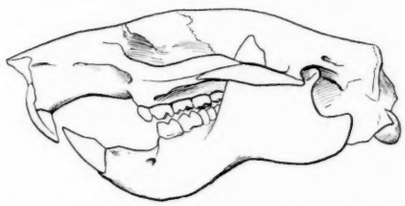


FIG. A. Skull and jaws of *Titanotheriomys*, approximately natural size.

Titanotheriomys Matthew, Bull. Amer. Mus. Nat. Hist., Vol. XXVIII, No. 6, 1910.
Genotype: *Ischyromys veterior* Matthew 1903.

The pre-orbital portion of the skull is much shorter than in *Ischyromys*. The nasals are broad, ending distinctly posterad of the anterior end of the zygoma. There is a broad flat area between the temporal crests, which do not unite to form a sagittal crest. The interorbital region is wide. The braincase is about as long as in *Ischyromys*, but more slender. The occiput slopes forward rather than being vertical. In lateral view, the skull is quite flat and low. The masseteric plate slopes much more than in *Ischyromys*, and there is a broad surface below the infra-orbital foramen. The masseter extends slightly laterad of the foramen, and occupies the plate below it. The zygomasseteric area is distinctly suggestive of that of a primitive "Sciuromorph." The area of masseteric origin on the ventral surface of the zygoma is distinctly limited. The mandible is smaller and proportionately more slender than in *Ischyromys*, the ascending ramus beginning slightly further posterad. The upper incisors are more sharply curved than in *Ischyromys*. The paracone is concave buccally. The lower teeth are narrow, especially $M\underline{2}$–$\underline{3}$.

The anterior cingulum of the upper teeth is very broad, and the metaloph has a distinct bend at its middle. The lateral surface of the paracone is concave, forming a notch in the margin of the tooth. The protocone and hypocone of $P\underline{4}$ are fully separated—as

much so as in the molars, thus representing an advance in specialization over *Ischyromys*. $P\underline{4}$ has a posterior cingulum (Pl. XXVII, Fig. 1*a*). The protocone and hypocone of the molars are more separate than in *Ischyromys*, though otherwise these teeth seem quite similar in the two genera. $DP\underline{3}$ has a heavier cingulum than does $P\underline{3}$. $DP\underline{4}$ has essentially the same pattern as $M\underline{1}$, differing chiefly in the slightly larger anterior cingulum and parastyle, and the more highly notched paracone. In addition, the separation of the protocone and hypocone is accentuated, so that the tooth is distinctly bilophate. The lophs are straighter than in the molars.

$P\overline{4}$ has a metalophulid II, but no metalophulid I, the anterior arm of the protoconid running down to the base of the metaconid, thus differing from *Ischyromys*. In some specimens, there is a conulid on the hypolophulid I. The hypoconulid is poorly developed. It is larger on the molars, but small even there, being nowhere near as large as in *Ischyromys*. The teeth, especially $P\overline{4}$ and $M\overline{3}$, are much narrower than in *Ischyromys*, this being, in fact, one of the most strikingly clear generic characters, and one listed by Matthew (1903, p. 211; 1910, p. 63). I have been entirely unable to find the difference in pattern of $M\frac{3}{3}$ which Matthew (1903, p. 212) indicated as distinguishing this form from *Ischyromys*. The pattern of the molars, except for the small hypoconulid, is similar to that of *Ischyromys*, though the teeth are lower crowned, with apparently higher cusps. The milk tooth seems indistinguishable from that of *Ischyromys*.

The lower incisors seem identical with those of *Ischyromys*. The jaw is distinctly more slender than in the latter genus, but is otherwise apparently identical.

There are certain badly damaged specimens in the author's collection, from the Middle Oligocene, south of Scenic, S. D., that have a narrow $M\overline{3}$ and a shallow jaw, thus suggesting *Titanotheriomys*.

While the skull is distinctly smaller than that of most species of *Ischyromys* (probably being about the same size as the unknown skull of *I. parvidens*), the greatest difference is in proportions. The braincase is nearly as large as in the Middle Oligocene forms. The orbit is smaller, but the snout is very much shorter, *Titanotheriomys* being extremely short-faced. The postorbital constriction is not as great as in *Ischyromys*, and the temporal crests do not meet to form a sagittal crest, but remain far apart, the intervening space being quite flat. The crests approach closest together in the area of the postorbital constriction, and thereafter diverge to the level of the glenoid, behind which they converge once more, resembling in a general way those of *Prosciurus* (Pl. XXIII, Fig. 1). The zygoma is very slender and plate-like when viewed from above, quite different from the heavy zygoma of *Ischyromys*, with its triangular cross section. The skull is broad and flat, rather than rounded as in *Ischyromys*. The interparietal is not distinct, being fused with the parietals, a condition that I have never observed in *Ischyromys*. The occiput slopes forward, the condyles being more visible in dorsal view than is the case in any specimen of *Ischyromys* that I have seen. The lachrymal has a distinct process extending over the orbit, instead of being flush with the edge of the orbit, as in *Ischyromys*. It is even more nearly separated from the frontal, on the skull top, by the maxillary, than in *Ischyromys*, but it has a long posterior process within the orbit, not seen in the latter genus.

The zygomasseteric region is quite different from that of typical *Ischyromys*, being approached only in *I. troxelli*. The palatine part of the maxillary forms a considerable

portion of the floor of the orbit in both genera. In *Titanotheriomys*, however, the masseteric plate of the zygoma also forms a considerable part of the floor, as opposed to *Ischyromys*, where there usually is no such plate. The infra-orbital foramen is visible in dorsal view in *Titanotheriomys*, which it is not in *Ischyromys*. The anterior face of the zygoma, in lateral view, is at about the same angle with the long axis of the skull in both forms. In *Titanotheriomys*, however, the area of origin of the masseter, below and behind the infra-orbital foramen, continues the slope of the anterior face of the zygoma, instead of being horizontal, as in *Ischyromys*. This plate closely resembles the lower part of the masseteric plate in "Sciuromorphs." In *Ischyromys*, the area of origin of the masseter is sharply limited to the ventral surface of the zygoma, posterior to and below the infra-orbital foramen. This area is not horizontal, but slopes upward at a lesser angle than in *Titanotheriomys*. In this latter, however, the crest marking the lateral limit of the masseteric fossa on the zygoma is continued laterad of the infra-orbital foramen, with what appears to be a fossa for a thin strip of the masseter, extending well forward of the infra-orbital foramen. This is extremely suggestive of the conditions in "Sciuromorphs," which could be derived from this type simply by enlarging this antero-external slip, thus forcing the infra-orbital foramen down on the face, and causing the development of a division between the fossa and the foramen, such as the countersinking of the foramen visible in the geomyoids, or the protective crest of the sciurids and castorids.

The bearing of this condition in *Titanotheriomys* on the classification of the rodents is at once obvious. Miller and Gidley (1918) have used the structure of the zygomasseteric region as the fundamental basis for rodent classification, basing five major groups on five different relationships between the masseter, the zygoma and the infra-orbital foramen, and stating (op. cit., p. 431) that "there is no evidence that any rodent during its development has passed from one to another" of these five categories. As they include the Ischyromyidae under the Muroidae (although the infra-orbital foramen in the ischyromyids does not transmit any portion of the masseter as it does in the muroids), and as *Titanotheriomys* falls within the limits of the Sciuroidae (by their definition), it is apparent that, if their assumptions and classification are correct, *Titanotheriomys* must be a case of a sciuroid exhibiting marvellous parallelism to *Ischyromys*. It seems to me, however, that it is much easier to assume the necessary incipient parallelism of the zygomasseteric structures than the tremendous parallelism, otherwise required, of teeth, jaws, palate and ear, especially since we really know nothing of the origin of the different types of zygomasseteric structure.

Of course, nothing is further from my intentions than to imply that in *Titanotheriomys* we have a phylogenetic link between the "Sciuromorpha" and the Ischyromyoidea. In view of the full development, by John Day time, of a typical sciuroid zygomasseteric pattern, I should expect to find the Lower Oligocene squirrels further advanced in this respect than is *Titanotheriomys*. Furthermore, the occurrence of eomyids with the "Sciuromorph" infra-orbital pattern in the same beds as *Titanotheriomys* entirely rules it out from possible ancestry to the "Sciuromorphs," if they are a monophyletic group. This conclusion is supported by the dentition, skull and skeleton of *Titanotheriomys*, which are those of a typical ischyromyid. Therefore we must add this genus to the already long list of instances of interesting and striking parallelisms between distinct lines of rodents.

There are a number of skeletal fragments in the American Museum, from Pipestone Springs, similar to corresponding bones in the skeleton of *Ischyromys*, but considerably

smaller and proportionately more slender, which are almost certainly referable to *Titanotheriomys*. This more slender quality is most clearly visible in the tibia. The fragments of scapula, humerus, ulna, femur, fibula, calcaneum and astragalus are extremely similar to those of *Ischyromys*. The sculpture of the calcaneum is distinctly finer than in *Ischyromys*.

This genus, while in itself not adding to the complexity of rodent classification, in that it is readily included among the Ischyromyidae, illustrates the extreme difficulty, at the present time, of promulgating a satisfactory classification of this order, and proves conclusively (if such proof were still considered necessary) that it is utterly impossible to develop a natural classification of the rodents on the basis of any single character or associated group of characters, but that the only method with any prospect of success is to base the classification on the entire anatomy of the animal, in so far as is known or knowable. Naturally, this will require careful and detailed studies of all available material, which is a work to occupy all students of the problem for years to come.

Titanotheriomys veterior (Matthew)

(Figs. 26–27, and Pl. XXVII, Figs. 2–4)

Ischyromys veterior, Matthew 1903, Bull. Amer. Mus. Nat. Hist., Vol. XIX.
Ischyromys (*Titanotheriomys*) *veterior* Matthew, Matthew 1910.
Titanotheriomys veterior (Matthew), Miller and Gidley 1920.

Lectoholotype: I designate Amer. Mus. No. 9658, lower jaw with $P\bar{4}$–$M\bar{3}$ left.

The lower cheek teeth are at least as long as broad in this species, and frequently longer. This emphasizes the generic character of narrowness of the teeth. The holotype has a partial barrier across the median valley of the molars, arising from the entoconid. This has not been observed in *T. wyomingensis*. It is very suggestive of the similar barrier sometimes present in *Ischyromys*. The notches in the paracones are deep. The zygomasseteric area is more nearly like that of *Ischyromys* than is the case in the other species of the genus. The pit in front of $P\underline{3}$, on the palate, is more shallow than in the other species.

FIG. 26. *Titanotheriomys veterior* (Matthew). Amer. Mus. No. 9720, $dP\underline{3}$–$M\underline{2}$ left.
FIG. 27. *Titanotheriomys veterior* (Matthew). Lectoholotype. Amer. Mus. No. 9658, $P\bar{4}$–$M\bar{3}$ left.
Both figs. × 5.

Matthew (1903, pp. 211–212) described this form, from the Titanotherium Beds of Pipestone Springs, Montana, as *Ischyromys veterior*, mentioning that there were in the

American Museum collections the anterior part of a skull and some forty jaws or parts of jaws, upper and lower. He characterized the form as being smaller than *I. typus*, with narrower teeth bearing higher cusps. He thought it was much closer to *I. cristatus* than to *I. typus*, but that it differed in having a less complete posterior cingulum on $M\frac{3}{3}$. In 1910 (p. 63), he raised this species into a subgenus of *Ischyromys*, *Titanotheriomys*. In addition to the characters listed in 1903, he pointed out the narrow incisors, small muzzle, absence of sagittal crest, slender zygomata, and that the superior border of the masseter extended forward onto the muzzle. To this species he referred Amer. Mus. No. 14,579, a skull and skeleton from the Titanotherium Beds of Wyoming. This last is now selected as the holotype of *T. wyomingensis* (see below, p. 198). The best skeletal material associated with *Titanotheriomys* specimens in the American Museum collections is from the Thompson Creek Beds, referred above to *Ischyromys pliacus*. Probably erroneously associated with this skeletal material was the anterior part of the skull of a young individual of *Titanotheriomys*, apparently the specimen Matthew mentioned in 1903. A number of isolated limb bones from Pipestone are referred to this species on the basis of size.

Range: Lower Oligocene of Pipestone Springs and Thompson Creek.

MEASUREMENTS OF *Titanotheriomys veterior*

	Holotype, Amer. Mus. No. 9658	*Amer. Mus. No. 9720*	
		Left	*Right*
	mm.	mm.	mm.
$P\bar{4}$ a-p	e3.55		
width metalophid	2.58		
width hypolophid	2.70		
$M\bar{1}$ a-p	3.46		
width metalophid	3.23		
width hypolophid	3.38		
$M\bar{2}$ a-p	3.46		
width metalophid	3.32		
width hypolophid	3.20		
$M\bar{3}$ a-p	3.30		
width metalophid	2.98		
width hypolophid	2.63		
$P\underline{3}$ a-p		d1.60	—
width		d1.68	d1.67
$P\underline{4}$ a-p		d3.76	ed3.68
width protoloph		d2.90	—
width metaloph		d3.23	—
$M\underline{1}$ a-p		3.63	3.63
width protoloph		3.44	3.47
width metaloph		3.35	3.50
$M\underline{2}$ a-p		3.40	—
width protoloph		3.33	—
width metaloph		3.18	—

d = deciduous tooth. e = estimated.

Titanotheriomys wyomingensis sp. nov.

(Pl. XXVII, Figs. 1, 1*a* and 1*b*)

Holotype: Amer. Mus. No. 14,579, skull with associated lower jaws, collected by Walter Granger, Beaver Divide, Wyoming, in 1909.

This species differs from the genotype in a number of characters. The notches in the paracones are much shallower in this form. The lower teeth are no longer than they are broad, and their narrow character is but little emphasized. There is a deep pit just anterad of P3. The zygomasseteric area has numerous striking parallelisms to that of the "Sciuromorphs," as has been pointed out above (p. 195). This species would then be a Protrogomorph that has developed the same muscular modifications as characterize the "Sciuromorphs."

Granger (1910, p. 241) says that "a fairly good skull and jaws with a considerable part of the skeleton of this genus was found" at Beaver Divide. I have been unable to find any trace of the skeleton, other than a fragment of the atlas.

MEASUREMENTS OF *Titanotheriomys wyomingensis*

	Amer. Mus. No. 14,966	*Amer. Mus. No. 14,580*
P4 a-p	3.43 mm.	mm.
width protoloph	3.95	
width metaloph	3.70	
M1 a-p	3.02	
width protoloph	3.99	
width metaloph	3.73	
M2 a-p	3.04	
width protoloph	3.51	
width metaloph	3.22	
M3 a-p	2.99	
width protoloph	3.27	
width metaloph	2.59	
P4–M3	12.70	d12.32
P4 a-p	3.58	d 2.97
width metalophid	2.39	d 1.93
width hypolophid	2.82	d 2.33
M1 a-p	2.95	2.96
width metalophid	3.03	2.90
width hypolophid	3.07	—
M2 a-p	3.04	3.06
width metalophid	3.37	3.00
width hypolophid	3.12	2.62
M3 a-p	3.48	3.22
width metalophid	3.10	2.93
width hypolophid	2.77	2.38

d = deciduous teeth.

Family Cylindrodontidae Miller and Gidley 1918

The family may be defined as follows: fossorial forms; cheek teeth $\frac{4}{4}$, mesodont to hypsodont and evergrowing; lower teeth with metalophulid I; no mesocone or mesoconid; infra-orbital foramen piercing wide zygomatic plate and transmitting no muscle.

As no portions of the post-cranial skeleton have as yet been described for members of this family, it is not surprising that the definition is still rather inadequate.

Range: Oligocene of North America and Asia.

Genera: *Cylindrodon, Pseudocylindrodon, Sespemys, Ardynomys, Cyclomylus* and *Tsaganomys.*

"*Cylindrodon, Pseudocylindrodon,* and *Ardynomys,* are probably Oligocene representatives of the stock of rodents typified in the Bridger Eocene by the forms which Troxell has included under *Tillomys.* In North America this line appears to culminate in the Lower Oligocene, at which time it is also represented by *Ardynomys* in Asia. Whether or not *Tsaganomys* and *Cyclomylus* of the Upper Oligocene of Mongolia are also derivatives of this stock is not determinable without further study, although there are some interesting points of resemblance between the latter genera and *Ardynomys*" (Burke, 1935, pp. 3–4). Certain preliminary work that I have begun on *Tsaganomys* and *Cyclomylus* shows the correctness of Burke's suggestion of their relationship to *Ardynomys.*

Matthew (1903, pp. 212–213) referred *Cylindrodon* to the Castoridae. He pointed out the absence of $P\bar{3}$, but indicated that he thought the pattern of the teeth was fundamentally similar to that of beavers. Incidentally, Matthew here (p. 213) points out the great difficulties in deriving later rodent tooth patterns from that of *Paramys.* In 1905, Lambe referred to the Cypress Hills specimen as belonging to a distinct species of *Steneofiber.* In 1910, however, Matthew (1910, p. 64) showed that the structure of the zygomasseteric area separates *Cylindrodon* from the Castoridae, and also indicated differences between this form and the ischyromyids. He referred it, however, provisionally to the Ischyromyidae, though with a suggestion that it should be separated as a distinct family, a step which was taken by Miller and Gidley (1918). In spite of this, numerous authors continue to refer this genus to the Castoridae. Stirton (1935) in his revision of the beavers, makes no mention of the genus, indicating his agreement with those authors who can see no signs of beaver relationships in *Cylindrodon.*

Little is known of the ancestry of the cylindrodonts other than their similarity to certain Middle Eocene sciuravids. A recent summary by Burke is the most complete discussion of this problem. "Wilson [1935] has recently suggested that *Pareumys* 'is quite possibly ancestral to *Cylindrodon.*' I am not disposed to take this position regarding the advanced *Pareumys milleri* Peterson, which appears to me to be trending in the way of an Ischyromys-like dentition, or even toward *Pareumys grangeri,* which seems to be evolving in the same general direction. However, it seems to me that *Pareumys* (?) *troxelli* has attained various characters which, by further specialization, might have resulted in the *Cylindrodon* type of dentition; the Uinta species, in other words, has the structural possibilities of evolution toward *Cylindrodon.* Yet I do not think that we should regard it, for the present, as anything more than a structural ancestor of *Cylindrodon.* Lower Oligocene rodents, such as *Ardynomys, Pseudocylindrodon,* and other forms as yet undescribed, contemporaries of *Cylindrodon* and much less specialized, preserve various struc-

tures 'ancestral' in essentially the same sense, to those of *Cylindrodon*. And I cannot escape the conviction, gained from observation of the tempo of rodent evolution in a few cases where we have fair evidence of direct descent, that the ancestor of *Cylindrodon* in the Upper Eocene had progressed beyond the stage represented in *Pareumys* (?) *troxelli*." (Burke, 1935*b*, p. 12.)

Even though the ancestry of the cylindrodonts cannot be considered as having been established, it must be regarded as extremely significant that as careful a student as Burke believes that a form which he refers to the Ischyromyidae is a close relative and structural ancestor of the Cylindrodontidae. Whether the lines of the Ischyromyidae and Cylindrodontidae converged before they both became merged in the presumably ancestral stock of the Sciuravidae is a question that cannot be answered even tentatively at the present time. The close relationship of these three families, however, may be considered as being definitely beyond question. They certainly belong to the same superfamily, though whether they should be united with the aplodontoids as a single superfamily, or grouped together as the Ischyromyoidea, is at present a matter of personal opinion.

Cylindrodon Douglass

(Figs. 28–30, 32, Pl. XXIV)

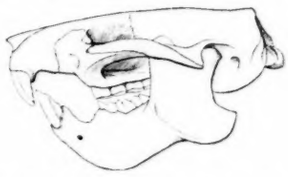


FIG. B. Skull and jaws of *Cylindrodon*, approximately natural size.

Cylindrodon Douglass, Trans. Amer. Phil. Soc., Vol. XX, 1902.
Genotype: *C. fontis* Douglass 1902.

The cheek teeth are high crowned, with deep basins, the floors not being visible in the crown view of unworn teeth. The protolophulid II is incomplete. The hypolophulid I is present on all the teeth. The central basin is narrow, whereas the anterior and posterior ones are broad. In the lower teeth, there is no mesostylid, the central valley thus opening freely linguad, whereas in the upper teeth, the basin is completely dammed by mesostyles. The posterior basins are open on M$\overline{1}$–$\overline{2}$, separating the entoconid from the posterolophid. The talonids of all the teeth are wider, but not greatly wider, than the trigonids. The hypoconids are compressed antero-posteriorly. There is a single mental foramen, below the diastema. The skull and incisors indicate that the animal was fossorial, though not extremely so.

This genus has been found in the Lower Oligocene of Montana, Wyoming, Saskatchewan and Colorado, and possibly of other states.

Cylindrodon, as indicated by Burke (1935*b*, p. 3) represents one extreme of the evolutionary adaptations of the family. The narrow talonids and the extremely rounded incisors are illustrative of this. In other characters, as the extreme hypsodonty, the fossorial adaptations of the skull, etc., this genus is distinctly more primitive than the later Mongolian members of the family, although it approaches them in many respects. *Cylindrodon*

differs from *Tsaganomys* and *Cyclomylus*, however, in that the crown has taken part in the hypsodonty, and the pattern persists for a long time, whereas, in the Mongolian forms, the pattern becomes very abbreviated, and is soon worn away, leaving only a pattern such as that which gave its name to the American genus. This difference in the depth to which the pattern extends is similar to the difference between *Heteromys* and *Dipodomys*, among the Heteromyidae.

The incisors, both upper and lower, are almost equidimensional, with gently rounded anterior faces. They are not particularly procumbent, which would seem to indicate that *Cylindrodon* was not a highly specialized burrowing form, in spite of the frequent assumption to the contrary.

In the upper cheek teeth, as well as in the lower, the central lake is retained the longest. There is only a single upper permanent premolar, though there are two upper deciduous ones. Worn upper teeth are essentially quadrate, and of uniform size. The enamel is retained, for a long time at least, of even thickness all around the crown. P$\underline{4}$ has a short anteroloph, reaching only to about the middle of the protoloph, and remaining free for a long time. The metaloph and posteroloph soon fuse. The molars have the same pattern as the premolar, as far as can be told from the available material, except for the anteroloph, which is as long as any of the other lophs, though it does not unite with the protoloph as early as do the two posterior lophs. The crown in unworn teeth, instead of being equidimensional, is very much longer than it is wide. The hypocone is slightly, though clearly, separated from the protocone. It also extends somewhat further linguad. The lophs are all fully developed in an unworn tooth, though the metaloph is slightly lower than the others. There is a clear metaconule, but there does not seem to be any protoconule. The anterior cingulum ends in a large and distinct parastyle. There is a small mesostyle but no metastyle. Neither is there any distinct hypoconule.

One specimen, Amer. Mus. No. 14,575, from Beaver Divide, Wyoming, shows the milk teeth. There was a minute dP$\underline{3}$, a simple conical tooth with no cingula at all (Fig. 29). DP$\underline{4}$ is very like M$\underline{1}$, differing in being slightly smaller and with a smaller metaconule.

As is so frequently the case among the rodents, the lower teeth are essentially mirror images of the upper. For a discussion of the details of the lower teeth, see Burke (1935*b*).

As pointed out by Douglass (1902) and Matthew (1904, p. 212), the pattern of worn teeth of this form is reduced to an enamel outline with, for a considerable period of time, only a single lake, representing the remains of the central valley. Burke (1935*b*) has emphasized the high crowns of *Cylindrodon*, and has pointed out the characteristic features of the tooth pattern, among which may be noted the variability of pattern of dP$\overline{4}$, which sometimes has a complete hypolophulid I as in P$\overline{4}$, and sometimes has this crest interrupted, as in P$\overline{4}$ of *Pseudocylindrodon*.

The infra-orbital foramen is small and high on the face. As the zygoma extends well down by the cheek teeth, there is a broad area below the foramen, very similar in shape and relationships to that of *Tsaganomys* (Matthew and Granger, 1923*a*, Fig. 3). In both, there is a broad plate of the zygomatic arch laterad of the infra-orbital foramen. In both, although the maxillary spreads out in a broad plate surrounding the foramen, the masseter is entirely limited to the ventral surface of the zygoma. This gives a peculiar appearance to the whole front of the skull, which is not duplicated outside of this family. The palate is short, ending by the rear of M$\underline{2}$. The sagittal crest is low, bifurcating just in front of

the postorbital constriction. At this latter point, the skull is quite wide. The zygomata are flaring. The braincase is broad and flat, the bullae large.

The jaw is short and massive (Pl. XXIV, Fig. 1), the diastema in particular being extremely short. The ascending ramus begins by the anterior end of $M\overline{2}$. The masseteric fossa is large, and distinctly angulate at the front end. There is no fossa behind the symphysis for the geniohyoid muscle.

Cylindrodon fontis Douglass 1902

Cylindrodon fontis Douglass, Trans. Amer. Phil. Soc., Vol. XX, 1902.

(Fig. 32; Douglass, 1901, Pl. 9, Figs. 9, 9*a*; Matthew, 1903, Figs. 7–8; and Burke, 1935, Fig. 2)

Holotype: Carn. Mus. No. 38.

The talonid of $M\overline{3}$ is wider than the trigonid. The protolophulid II of the molars runs antero-linguad. $DP\overline{4}$ is not yet molariform, the entoconid not being connected with the hypoconid, and its trigonid is quite small.

Range: Titanotherium Beds of Pipestone Springs, Montana and the Thompson Creek Beds of Montana.

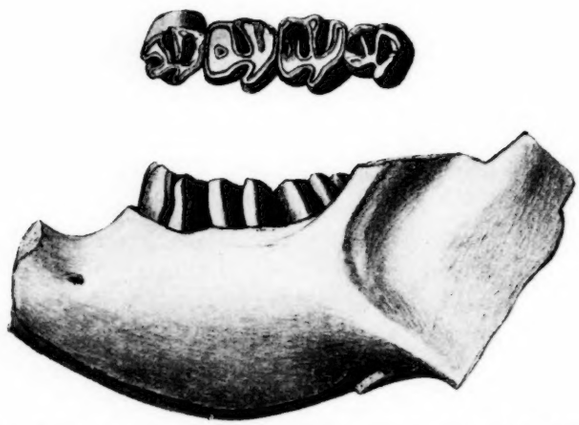


FIG. 32. *Cylindrodon fontis* Douglass. Amer. Mus. No. 9638, $P\overline{4}$–$M\overline{3}$ left, and external view of ramus. After Burke, 1935*b*, Fig. 2. × 5.

Cylindrodon aff. fontis

Cylindrodon fontis Douglass, Lambe 1908.

(Fig. 28; and Lambe, 1908, Pl. VIII, Figs. 19–20)

This specimen is Can. Nat. Mus. No. 6481, a fragment of the left mandible with $M\overline{1}$, the alveolus of $M\overline{2}$ and parts of the alveoli of $P\overline{4}$ and $M\overline{3}$, collected four miles above East End Post Office, Cypress Hills, Saskatchewan.

The tooth is high crowned as in *Cylindrodon fontis*. It possesses, however, a hypoconid produced well laterad as in *Pseudocylindrodon* (Burke, 1935*b*, p. 2), and the posterior valley is more closed than in *C. fontis*, though less so than in *P. neglectus*. In spite of the hypoconid being hypertrophied as in *Pseudocylindrodon*, it is narrow and compressed anterc-posteriorly as in *Cylindrodon*. The entoconid has not moved forward as in *C. fontis*, the hypolophulid I running directly across the tooth.

The fragment of the mandible does not show any mental foramina, suggesting that the foramen was placed well forward as in *C. fontis* rather than as in *Pseudocylindrodon*, since the posterior of the two in the latter form would show on the part of the mandible preserved, if it had existed. In shape, the masseteric fossa (Lambe, 1908, Pl. VIII, Fig. 19) seems more like that of *Cylindrodon* than like that of *Pseudocylindrodon* (Figs. 32–33).

The tooth measurements of this specimen essentially agree with those of *C. fontis*, the only appreciable difference being the increased width of the hypolophid.

The measurements of this specimen are as follows:

	$M\bar{1}$	$M\bar{2}$	
antero-posterior	2.20 mm.	2.18 mm.	(of the alveolus)
width metalophid	1.78	2.55	(of the alveolus)
width hypolophid	2.18	2.55	(of the alveolus)

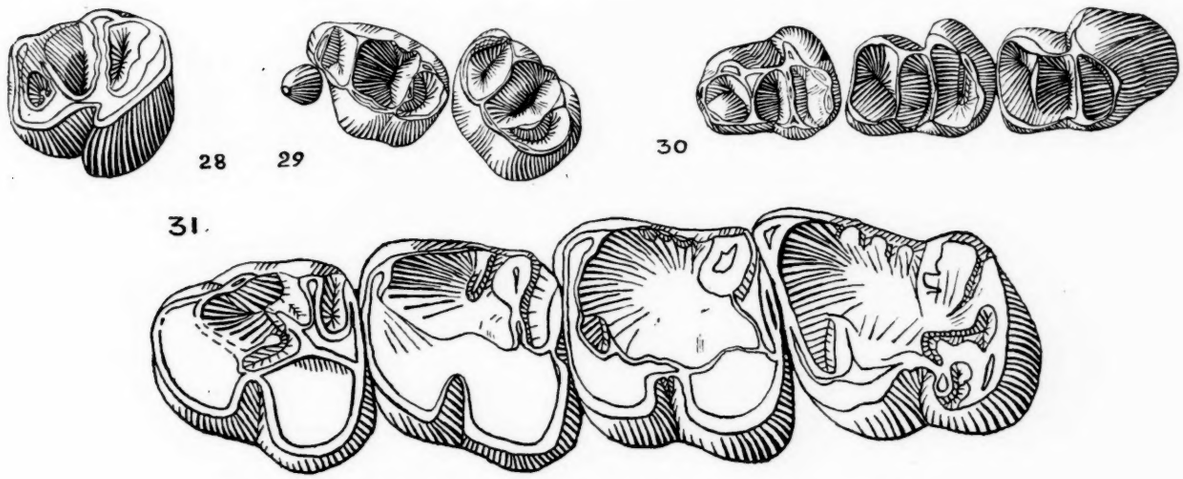


FIG. 28. *Cylindrodon* cf. *fontis*. Can. Nat. Mus. No. 6481, $M\bar{1}$ left.
FIG. 29. *Cylindrodon* n. sp. Amer. Mus. No. 14,575, $dP\underline{3}$–$M\underline{1}$ left.
FIG. 30. *Cylindrodon* n. sp. Amer. Mus. No. 14,575, $dP\bar{4}$–$M\bar{2}$ right.
FIG. 31. ?*Sespemys* sp. M.C.Z. No. 5056, $P\bar{4}$–$M\bar{3}$ left.
All figs. × 10.

Cylindrodon sp. nov.

(Pl. XXIV, Figs. 1, 1*a* and 1*b*, and Text Figs. 29–30)

There are six specimens of a cylindrodont from the Lower Oligocene of Beaver Divide in the American Museum collections, including partial skulls of three individuals and lower jaws of four. These belong to a form close to *C. fontis*, but seem to be appreciably different. The talonid of $M\bar{3}$ is much narrower than in *C. fontis*, the mental foramen seems further posterad, the teeth, when worn, seem more quadrate, and $dP\bar{4}$ is much more molariform. The protolophulid II runs straight across the tooth, instead of trending forward, as in *C. fontis* from Pipestone. It is one of these Beaver Divide specimens that shows the previously unreported $dP\underline{3}$ (Fig. 29). The lower incisor is distinctly broader and flatter than in *C. fontis*. The fossa behind the symphysis is also distinctly stronger and deeper.

MEASUREMENTS OF *Cylindrodon* n. sp.

	Amer. Mus. No. 14,575		*Amer. Mus. No. 14,575*
$P\underline{3}$ a-p	d0.55 mm.	$P\overline{4}$ a-p	d2.00 mm
transverse	d0.53	width metalophid	d1.29
$P\underline{4}$ a-p	d2.04	width hypolophid	d1.57
width protoloph	d1.54	$M\overline{1}$ a-p	2.00
width metaloph	d1.47	width metalophid	1.36
$M\underline{1}$ a-p	2.06	width hypolophid	1.63
width protoloph	1.49	$M\overline{2}$ a-p	2.00
width metaloph	1.61	width metalophid	1.45
		width hypolophid	1.70

d = deciduous tooth.

Range: Lower Oligocene of Beaver Divide, Wyoming.

Pseudocylindrodon Burke 1935

Pseudocylindrodon Burke, Annals Carn. Mus., Vol. XXV, 1935.

Genotype: *P. neglectus* Burke 1935.

(Fig. 33; Matthew, 1903, Fig. 8A; and Burke, 1935, Fig. 1)

"Cheek teeth with lower crowns than those of *Cylindrodon*, and with shallower basins, the floors of which are visible in crown view. $P\overline{4}$ with trigonid more elevated than in *Cylindrodon* and trigonid cusps less widely separated, protolophid [protolophulid II] absent or merely indicated, external intermediate cuspule present but hypolophid absent. Inferior molars with central basins broader, anterior and posterior basins narrower, anteroposteriorly, than in *Cylindrodon;* internal intermediate cuspules prominent, their flanks fused with entoconids and metaconids, blocking outlets of central basins; posterior basins converted into fossettes, their outlets dammed due to complete fusion of entoconids and hypolophulid crests [= posterolophids]. Talonids of molars, except in $M\overline{3}$, wider, relative to trigonids, than in *Cylindrodon;* hypoconids showing some hypertrophy, consisting of strong rounded buttresses, jutting externally (except in $M\overline{3}$) and not attenuate as in *Cylindrodon.* $DP\overline{4}$ relatively smaller than in *Cylindrodon.* Mental foramina two, placed posterior to diastema." (Burke, 1935*b*, pp. 1–2.)

Pseudocylindrodon seems a survival of the ancestral stock from which *Cylindrodon* was derived, but it has developed a few peculiarities of its own. "In some respects, *Pseudocylindrodon* is intermediate between *Cylindrodon* and *Ardynomys.* The cheek teeth are nearer those of *Ardynomys* in crown height and their tendency toward hypertrophy of the hypoconid region; the tooth pattern in general shows similarities. The incisor of *Pseudocylindrodon* is not flattened, however, as it is in *Ardynomys;* the central basins of the cheek teeth are deeper in *Pseudocylindrodon,* have rounded floors, and are closed internally by the upgrown intermediate cuspule. The jaw of *Ardynomys* is deeper anteriorly than that of *Pseudocylindrodon,* the posterior basins of the cheek teeth of *Ardynomys* have internal exits, and the protolophids [= protolophulid II's] are less transverse than in *Pseudocylindrodon.*" (Burke, op. cit., p. 3.)

At present, *Pseudocylindrodon* is unfortunately known only from mandibles, and only from one locality, the Lower Oligocene of Pipestone Springs, Montana.

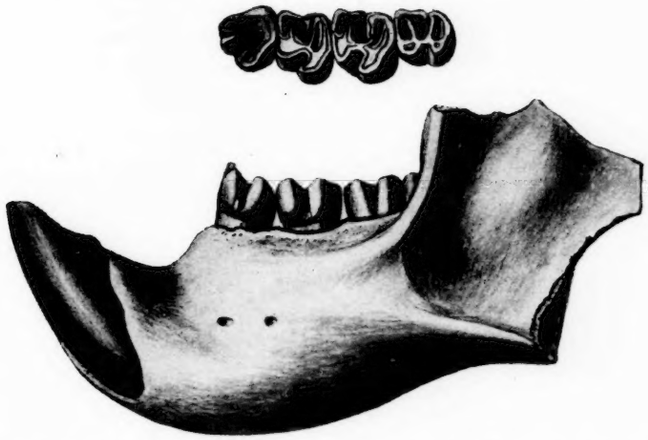


FIG. 33. *Pseudocylindrodon neglectus* Burke. Holotype. U.S.N.M. No. 13,758, $P\bar{4}$–$M\bar{3}$ left and external view of ramus. After Burke, 1935*b*, Fig. 1. × 5.

Pseudocylindrodon neglectus Burke 1935

Pseudocylindrodon neglectus Burke, Annals Carn. Mus., Vol. XXV, 1935.

Holotype: U.S.N.M. No. 13758, lower jaw with $P\bar{4}$–$M\bar{3}$ left.
Paratype: left lower jaw, U. S. Nat. Mus. No. 13,757.

Since this is the only species of the genus now known, it cannot be discussed separately from the genus.

Ardynomys Matthew and Granger, 1925

Ardynomys Matthew and Granger, Amer. Mus. Novitates No. 193, 1925.

Until recently, this genus has been considered as being solely Mongolian. Since this paper was written, a description has appeared of a member of this genus in the North American Oligocene (Burke, 1936). I have not had an opportunity to examine the American specimens of this genus, so must rely on quotations from Burke. *Ardynomys* is an intermediate stage in the series leading up to such specialized burrowing forms as *Tsaganomys*. It seems to be in the initial stages of fossorial development—perhaps similar in habitus to the prairie dog. On the other hand, it shows fundamental resemblances to the other cylindrodonts.

Range: Lower Oligocene of Mongolia and Montana.

Ardynomys occidentalis Burke, 1936

Ardynomys occidentalis Burke, Annals Carn. Mus., Vol. XXV, 1936.

(Burke, 1936, Figs. 1–5)

Characteristic of this species are "the robust construction throughout, the flattened brain-case, the sharply constricted and narrow interorbital region, and the antorbital breadth, coupled with an angular and heavy type of rostrum. . . . The brain-case was

somewhat wider than the rostrum. . . . A small post-glenoid foramen is shown, posteromedian to which occurs a large subsquamosal foramen. . . . The brain cast . . . indicates that this region of the skull must have been flattened to a degree comparable with the same region in the skull of *Aplodontia*. This cast shows broad cerebral lobes and a fairly distinct superior longitudinal fissure, but the hemispheres have not the heart-shaped anterior tapering which characterizes *Cynomys* and *Ischyromys*, and, but to a lesser degree, *Aplodontia;* the outline is decidedly more rounded and becomes almost truncate directly behind the olfactory bulbs. . . . The . . . bulbs . . . are relatively large, apparently foreshortened longitudinally, expanded laterally and inflated. . . . The absence of the bones of the dorsal surface of the skull . . . exaggerates the interorbital constriction . . . , but . . . it is quite pronounced. The lateral walls of the brain-case round rather sharply forward to make the constriction, anterior to which the skull again fans outward fairly rapidly to the zygomatic region. There is no means of determining . . . whether postorbital processes were present or not. . . . On the right side, the naso-lacrimal foramen is shown. The lacrimal does not enclose the canal entirely; . . . in general its construction seems to be as in *Arctomys*. . . . In anterior view the skull of *Ardynomys* shows the zygomatic region . . . widely expanded; even in the absence of the malar, . . . this outjutting of the arch is pronounced. . . . It is most evident below, where it would probably be accentuated if the malar were preserved." (Burke, 1936, pp. 136–137.)

"There is a strong lateral expansion of the anterior zygomatic root, but the latter is heavy and sturdy, not thin and sharp as in *Tsaganomys*. . . . The upward tilt of the zygoma is more marked. . . . The infraorbital foramen is somewhat ovate, as in *Tsaganomys*. I cannot find any evidence that the infraorbital foramen (which is not enlarged) transmitted a slip of the masseter. The rostrum . . . is quite broad posteriorly and tapers fairly uniformly anteriorly. The premaxillaries reach to the interorbital region. . . . There is a prominent incisive swelling produced by a sharp outward arching of the premaxillaries. . . . The incisive foramina are of fair size and confined to the premaxillaries. The tooth rows diverge anteriorly. . . . The posterior palatal notch extends anteriorly to the posterior region of $M\underline{2}$; the palatines are short. . . . The slit-like posterior palatine foramina are located opposite the first molars." (Op. cit., pp. 138–139.)

"The incisors . . . are especially large when compared with the cheek teeth. The superior incisors are flattened along the anterior surface (showing only a slight rounding) and are a little more extended transversely than antero-posteriorly." (Op. cit., p. 139.) Burke also states (p. 142) that the lower incisor is very similar to that of *A. olseni*, having a flattened, and, in some specimens, even a faintly grooved, anterior face.

$P\underline{3}$ was "merely a slender spike which rested along the antero-internal side of $P\underline{4}$. $P\underline{4}$, on the other hand, was the largest tooth in the maxilla. . . . The cheek teeth . . . combine unilateral hypsodonty (by extension rootward of the crown enamel of the protomere) with oblique implantation. . . . With age, the teeth . . . show marked broadening of the protomere shelf, the crown surface of which is worn away long before that of the metamere." (Op. cit., p. 140.) Unworn molars are "subrectangular in outline. They taper somewhat rootward (especially $M\underline{1}$) when viewed internally. . . . The molar pattern . . . follows the same general plan as . . . $P\underline{4}$, consisting of anterior and posterior cingular crests, separated by anterior and posterior valleys from the protoloph and the metaloph. The latter lophs converge and extend to the internal shelf in the form of a

sharp V, enclosing between them the central valley. The shelf is not strongly bowed in outline at the crown surface, . . . a feature which contributes to the sub-rectangular outline of these teeth. In all of the molars the metaloph is somewhat oblique to the protoloph. The external outlets of the anterior and posterior valleys are nearly completely dammed off (except in M3, where the posterior valley exit cuts rather deeply), and are short notches considerably above the level of the central valley exit. The exits of the posterior valleys are in reality postero-external, internal to the metacones. The posterior valley extends further internally in these molars than does the anterior valley. The paracone and the metacone are nearly the same size in M1 but the paracone is in excess of the metacone in M2–3. There is a small intermediate tubercle in the outlet of the anterior valley of RM2 which is not present in . . . LM2. There is an intermediate tubercle in the outlet of the central valley of M1 which forms a dam; the same condition holds in M2. In M3 the intermediate tubercle is not present, but a small tubercle buds off the posterior flank of the metacone, somewhat crowding the exit of the posterior valley. A definite metaconule is not shown in M1 or in M2 although some swelling of the metalophs probably indicates it. In M3 it is indicated as a vanishing tubercle on the unworn metaloph. Incidentally, the metaloph in M3 sinks below the level of the triturating surface before connecting with the internal shelf—a condition which may have held, to some extent, in the metalophs of M1–2 before they were worn down. On the internal side, the molars show slight anterior and posterior enamel grooves or notches, between which the protocone swells internally.

"The lower jaw . . . is remarkably close to that of *Ardynomys olseni*. . . . The jaws are heavy and deep anteriorly; the masseteric fossa is not in advance of M$\bar{1}$. . . . The symphysis is extended downward to produce a sharp flange-like projection. There is a large mental foramen, below and just anterior to P$\bar{4}$. . . .

"P$\bar{4}$ . . . bears on the trigonid two cusps, which are separated by a notch-like median valley anteriorly. The internal of these two cusps is the larger and doubtless was, before wear, the higher of the two, as in *Ardynomys olseni*. . . . Its posterior flank is considerably drawn out to meet with the base of the postero-internal cusp, raising the internal outlet of the central basin high above the floor of the basin. The antero- and postero-external cusps are connected by an ectolophid.

"The hypoconid is an over-sized, jutting cusp, becoming a shelf with wear. From it extends a hypoconulid crest which sweeps around to join with the entoconid. The central basin is broad and rounded, and there is no definite evidence of any crests from the trigonid cusps within it. . . . [The hypolophid crest] on close inspection . . . can be detected forming the posterior boundary of the central basin. It is low, curling parallel with the hypoconulid crest, and is evidently being eliminated, although it still shows a connection with the entoconid. The posterior valley is little more than an entrenched shelf behind it. . . .

"The cheek teeth increase in size from P$\bar{4}$ to M$\bar{2}$; M$\bar{3}$ was considerably smaller than M$\bar{2}$. . . . The central . . . valleys have a V-shape with wear, and at their outlets are flanked by the entoconids and metaconids; the entoconids, on P$\bar{4}$, M$\bar{1}$ and M$\bar{2}$, do not extend as far internally as do the metaconids. . . . The unworn crown must have resembled rather closely that of *Ardynomys olseni*. . . . Not only is the hypoconid a greatly enlarged element of the crown in these teeth, but also the enamel extends disproportionately down along its enlarged root; one is tempted to call this 'unicuspal,' rather than unilateral, hypsodonty." (Burke, op. cit., pp. 140–144.)

On the basis of these characters as outlined above, Burke has re-emphasized the fundamental similarity of *Ardynomys* to the cylindrodonts, and its equally striking relationships to *Sespemys*. He then develops the exceedingly interesting thesis that the expansion of the more progressive Protrogomorphs in the Oligocene was correlated with the extinction of the highly specialized ground-dwelling paramyids at the close of the Eocene. But, as he states, in spite of the numerous parallelisms between these more specialized Paramyidae and the Oligocene Protrogomorphs, there can be no question of a special affinity between the two groups—merely another case of the usual rodent parallelism between members of related families.

The discovery of this Mongolian form in the American Oligocene, together with the European form described on a later page, merely add a few minor complexities to the exceedingly tangled web of rodent palaeontology.

Range: Lower Oligocene of McCarty's Mountain, Montana.

Cf. **Sespemys** Wilson 1934

Sespemys Wilson, Carn. Inst. Wash. Publ. 453, No. 2, 1934.

(Fig. 31)

The present specimen, Mus. Comp. Zool. No. 5056, is a right lower jaw from the Upper Brulé, 6 miles north of Bayard, Morrill County, Nebraska, collected by R. V. Witter in 1933. It is thus much later than the typical North American cylindrodonts, or than the Mongolian *Ardynomys*, but agrees closely with *Sespemys* in age.

This animal has a complete metalophulid I and a very weak metalophulid II. The hypolophulid is weak and seems to have been much as in *Prosciurus*. The mesoconid is small and subdivided, and there is no mesostylid. The posterolophid is short, not reaching the lingual side of the teeth. There are numerous minor irregularities in the enamel of unworn teeth, shown on $M\overline{3}$ of this specimen (Fig. 31). The Nebraska form differs from *Sespemys* in the absence of the mesostylid (Wilson's metastylid), the extreme weakness of the hypolophid, the tendency in *Sespemys* for the mesoconid to connect with the posterior arm of the protoconid, and the somewhat more complicated type of masseteric fossa. The incisor is rounded anteriorly instead of being flat as in *Sespemys*. There are several similarities to *Prosciurus*, with which Wilson compared *Sespemys*. The present specimen differs from *Prosciurus*, however, in the shape of the masseteric fossa, the absence of a mesostylid, but particularly in the small size of the mesoconid, a cusp that is particularly large in *Prosciurus* and sciuravids in general. The hypoconulid is essentially non-existent in this specimen, whereas it is fairly large in *Prosciurus*. From *Ardynomys* this form differs in the presence of a crest from the entoconid toward the hypoconid on $P\overline{4}$, even though it is incomplete; the presence of a mesoconid; the shape of the jaw and of the masseteric fossa, which is more sciuravid-like; the flatness of the incisor and the entire absence of any grooving; and the small size of the posterior arm of the protoconid, which does not unite with the metaconid. There are likewise certain superficial similarities to European fossils, such as *Plesiospermophilus*. Closer inspection, however, reveals important differences in the relations of the hypolophulid.

This animal belongs to a group of North American rodents, the presence of which had not been suspected in any post-Chadron deposits until quite recently. Just what the relationships either of this specimen, or of *Sespemys*, are, either to each other, to the Chadron forms, or to the Mongolian members of the family, is not at all clear.

MEASUREMENTS OF Cf. *Sespemys*

	Mus. Comp. Zool. No. 5056		*Mus. Comp. Zool. No. 5056*
$P\overline{4}$–$M\overline{3}$	12.45 mm.	$M\overline{2}$ a-p	3.05 mm.
$P\overline{4}$ a-p	2.99	width metalophid	3.27
width metalophid	2.35	width hypolophid	3.34
width hypolophid	3.00	$M\overline{3}$ a-p	3.63
$M\overline{1}$ a-p	2.81	width metalophid	3.27
width metalophid	2.80	width hypolophid	2.84
width hypolophid	3.13		

Suborder "SCIUROMORPHA" Brandt, 1851

Rodent families in which the masseter lateralis has grown up on the anterior face of the zygoma, causing a forward migration of the infra-orbital foramen, and forming a broad masseteric plate on the anterior face of the zygoma. Dental formula $P\frac{2-1}{1}$, $M\frac{3}{3}$.

Range: Upper Eocene to Recent of the entire world except Australasia and Oceanica.

While it is quite convenient to group these families together for the time being, it must constantly be borne in mind that there is no satisfactory evidence that their similarities are indicative of relationship and do not merely represent parallelisms of the rodent radiation, no more striking than a good many other parallel trends that are known to have had independent origins.

The above definition is purposely drawn to include only *families* with the "Sciuromorph" type of infra-orbital foramen typically developed, in order to exclude such obviously parallel developments as *Titanotheriomys* and any others that may be found in the future. This group is essentially identical with Miller and Gidley's Sciuroidae. I have used Brandt's terms since they have considerable priority, are just as convenient, and since I believe that these main groups are more readily considered as suborders than as superfamilies.

Superfamily GEOMYOIDEA

"Premolars reduced to $\frac{1}{1}$; cheek teeth primitively cuspidate and brachydont, progressively hypsodont and lophodont, first bilophate, then becoming enamel ovals, and finally reduced to enamel plates at one or both sides of the teeth; molars based on sextitubercular pattern, two of the cusps being derived from cingula; infraorbital foramen far forward on rostrum, about half way from zygoma to alveolus of incisor, not separated from masseter by large crests or ridges; mastoid greatly developed, and spread out onto occipital or dorsal surface of the skull, or both, with corresponding reduction of the occipital; large external fur-lined cheek pouches, supplied with musculature by the platysma and trapezius; external form murine or some modification thereof, but not sciurine; pelage without under fur." (Wood, 1935*a*, p. 80.)

Range: Middle Oligocene to Recent of North America and northernmost South America.

The two families that are referred to this superfamily are extremely closely related in

most of their anatomy, and are sometimes considered as being a single family. There are sufficient distinctions, however, and the palaeontological record shows that the separation has been of sufficiently long standing, to warrant the retention of the two as distinct families. The Oligocene representatives of the groups are few, and known only from fragments, but certain typical distinctions between the families appear even then. It seems likely that when skulls are found, further differences will be shown. However, there is no reason for not believing that the common ancestor of the two families lived relatively shortly before the time with which we are dealing in the present paper. The members of the superfamily are too poorly known in the White River to allow any phylogenetic conclusions to be based on them. In beds of Lower Miocene and later age, however, are a number of interesting forms that seem to be intermediate between typical heteromyids and geomyids, suggesting that there was as much polyphyly in the initial stages of the evolution of the group as there has been in the later stages within the separate families. Certain of these forms have recently been treated by Wood (1936*b*) and by Wilson (1936). Others are still undescribed.

What the pre-White River history of the geomyoids was, we cannot say at present. There are no known Eocene or Lower Oligocene rodents that seem to approach this group in the slightest degree. The entire absence of such fossils in North America might be taken for an indication of an Old World origin of the group, were it not that possible ancestors are equally absent in the collections from the Old World. Moreover, of course, there are no formations of the North American Tertiary the faunas of which are sufficiently well known to allow us to draw any conclusions of palaeodistributional significance from the absence of any given rodent or group of rodents from those beds. Our ignorance therefore compels us to leave the geomyoids completely without any possible ancestor for the present.

If the character of the infra-orbital foramen be taken as a diagnostic feature, these rodents are a superfamily of the "Sciuromorpha" as here defined. There is nothing in the rest of their organization diametrically opposed to this view, though many authors have considered the geomyoids to be "Myomorphs." They are here placed in the "Sciuromorpha" largely as a matter of convenience.

Family Heteromyidae Allen and Chapman 1893

The definition of the family as given by Wood (1935*a*, p. 81) may be quoted here. "Cheek teeth brachydont to hypsodont and even rootless; usually six cusps per molar, three on each loph; enamel rarely divided into two plates, never reduced to one; while the evolution of the teeth parallels that of the Geomyidae, at a given time the teeth of heteromyids are always more primitive; skull light, thin and papery; mastoids inflated, intermastoid diameter often being the greatest, never appreciably less than interzygomatic; interorbital space wider than rostrum; palate nearly horizontal, little if any below level of zygoma; nasals produced far beyond incisors; zygoma slender, with greatly reduced malar, almost, or quite, abutting against tympanic; frontals and parietals broad, the latter reaching, or nearly reaching, the orbits; frontal trapezoidal; parietal quadrate to pentagonal and triangular; interparietal primitively large, secondarily reduced; squamosal mostly or entirely confined to orbit; tympanic inflated or highly inflated, and vesicular; mastoids inflated and bullous, reaching top of skull, and forming part of occipital surface; occipitals contracted and limited in area on occiput, but extend onto dorsum of skull; small, sloping

coronoid processes, below the level of the condyle; jaw small and weak with large, everted angle; tail as long as, or longer than, head and body; claws of manus elongate, fossorial, but fore-limb slender; . . . body form murine to ricochetal."

Heliscomys Cope 1873*b*

Heliscomys Cope, Misc. Publ. U. S. Geol. Surv. Terr., 1873.

Genotype: *H. vetus* Cope 1873*b* from the Middle Oligocene Cedar Creek Beds of northeastern Colorado.

This form is minute, being the smallest of the White River rodents. $P\bar{4}$ is tricuspidate with a single anterior cusp, but progressively develops accessory cuspules. $M\bar{1}$–$\bar{2}$ are quadritubercular with a broad external cingulum, which divides to form two cusps, thus making each tooth sextitubercular. $M\bar{3}$ has only a single stylid, on the metalophid. $P\underline{4}$ has a reduced paracone and a weak internal cingulum. $M\underline{1}$–$\underline{2}$ have the same pattern as do the corresponding lower molars, except that it is reversed. There is no hypocone in $M\underline{3}$, but the cingulum is present. The teeth are bunodont and brachydont, and the cusps are not united to form lophs.

This genus is a good starting point for the evolution of the later Heteromyidae, with a tooth pattern which could easily give rise to that of any of the other members of the family, or, in fact, of the superfamily.

In *H. vetus* the cingulum of the molars is definitely lower than the other cusps, and is just beginning to divide. In *H. hatcheri*, the cingulum is still lower, and on $M\bar{1}$, shows hardly any trace of development of cusps. *H. senex* has reached about the same stage of development as has *H. vetus* in this character. The internal cingulum of the upper molars of *H. gregoryi* is much further advanced than is the corresponding cingulum of any of the other forms, the cingulum cusps being as large and as high as those of the protomere, though smaller than those of the paramere. The primary cusps of the molars are subequal in size in all members of the genus, are essentially conical, equally spaced, and the valleys between them are of almost equal depth, though the median valley is slightly the deeper, as is illustrated by the holotype of *H. hatcheri*. $M\bar{3}$ is somewhat smaller than the other molars, and shows the cingulum limited to the anterior half of the tooth. The four cusps are well developed, though those of the talonid are slightly smaller than those of the trigonid. This is rather different from the conditions in $M\underline{3}$, where the cingulum is continuous along the whole internal side of the tooth, and there does not seem to be any hypocone. Whether this is a specific difference between *H. senex* and *H. gregoryi*, or whether it is a difference between the upper and lower molars cannot be told at present, though the former seems somewhat the more likely. The Miocene heteromyids are too poorly known to help much with this problem.

The lower premolar of this genus is of considerable interest. As was pointed out by Wood (1935*a*, pp. 86–87, 210–211), *H. senex* seems to indicate a possible method by which the three cusped premolar of *H. vetus* may have given rise to the four cusped premolar of *Mookomys* and *Proheteromys*. This gap is by no means bridged at the present time, in view of the necessary assumption that, according to this hypothesis, a new cusp has developed at the antero-buccal corner of the premolar, forcing the previously central anterior cusp to the lingual side. This hypothesis is supported by the appearance of the tooth in *Proheteromys thorpei* from the John Day (Wood, 1935*b*, Fig. 1). If this interpretation is

correct, it makes it wholly impossible at present to correlate the cusps of the lower premolar with those of the corresponding tooth of other rodents. It is, however, true that with any other interpretation of these cusps, they are almost equally difficult to homologize with those of any other rodents.

Anterior cingula, of varying size, are present on all the molars, both upper and lower, of this genus.

The upper premolar is known only in *H. gregoryi*. It is primarily a four-cusped tooth, three cusps being present in a posterior semicircle, with the fourth between the horns of the crescent. The lingual cusp of the three posterior ones has been interpreted (Wood, 1933 and 1935*a*) as being of cingular origin, homologous with the lingual cusps of the molars. It shows, however, little or no definite trace of such an origin, and was merely assumed to be such by analogy with the molars, since there was no other plausible interpretation available. It seems best at present, however, to make no interpretations of the homologies of any of the cusps in either the upper or the lower premolars of *Heliscomys*. In *H. gregoryi*, there is a small antero-buccal cuspule on the premolar, the possible significance of which as indicating relationships with the Heteromyinae has already been discussed (Wood, 1935*a*, pp. 88, 209).

The maxilla, as far as known, is not appreciably different from that of the living *Perognathus* (Wood, 1933, p. 139). The jaws are low and slender and of typical primitive heteromyid construction. No specimens are known with complete mandibles.

Heliscomys vetus Cope 1873*b*

Heliscomys vetus Cope, Misc. Publ. U. S. Geol. Surv. Terr., 1873.

(Cope, 1884, Pl. LXV, Figs. 14, 16, 16*a* and 17; Wood, 1931, Fig. 2; Wood, 1933, Fig. 7; Frechkop, 1933, Fig. 7; Wood, 1935*a*, Fig. 7)

Holotype: Amer. Mus. No. 5461, lower jaw with $P\bar{4}$–$M\bar{1}$.

$P\bar{4}$ is tricuspid. In $M\bar{1}$–$\bar{2}$ the cingulum is lower than the four main cusps, and only incipiently divided into two cuspules.

Range: Cedar Creek Beds of northeastern Colorado.

Heliscomys gregoryi Wood 1933

Heliscomys gregoryi Wood, Jour. Mammalogy, Vol. XIV, 1933.

(Wood, 1933, Fig. 6; Frechkop, 1933, Fig. 7; Wood, 1935*a*, Fig. 6)

Holotype: Carn. Mus. No. 10,176, maxilla with $P\underline{4}$–$M\underline{3}$.

$M\underline{1}$–$\underline{2}$ are sextitubercular, with the cingulum cusps as large as the cusps of the protomere, but smaller than those of the paramere. $P\underline{4}$ is perognathine in aspect, but has a minute antero-external cuspule. $M\underline{3}$ has a continuous cingulum along the entire inner face, but shows no trace of a hypocone.

This form is important, being the only known maxilla of *Heliscomys*, and, with the exception of a single tooth in the author's collection, from the Big Badlands, the only known upper teeth of any member of the genus.

Range: Middle Oligocene Cook Ranch Beds of Montana.

Heliscomys hatcheri Wood 1935*a*

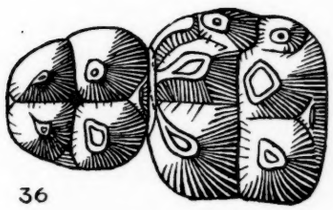
(Fig. 34, and Wood, 1935*a*, Fig. 6*b*)

Heliscomys hatcheri Wood, Annals Carn. Mus., Vol. XXIV, 1935.
Holotype: U.S.N.M. No. 6635, lower jaw with $M\bar{1}$–$\bar{2}$ right.

The teeth are square, with the external cingula smaller and less elevated than in any other member of the genus. The anterior cingula are likewise small. The antero-external cingulum of the lower teeth has two minor cuspules, and there is a deep valley, not well shown in the holotype (but see Fig. 34), between the protoconid and the protostylid. The hypoconid is far forward, as is suggested in the holotype, a condition rather distinct from what is seen in any other member of the genus. The referred lower teeth seem to have distinct heteromyine affinities. In the only known upper tooth (Fig. 34*c*), the cingulum is not as much divided as in *H. gregoryi*. The cusps of the metaloph are connected by a posterior cingular ridge. The cusps of the paramere are quite high. If I am correct in my reference of this upper tooth to *H. hatcheri*, as seems extremely probable, it means that the lower teeth of *H. gregoryi* must have been larger than those of any other species of the genus (see table of measurements).

34

35



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37

FIG. 34. *Heliscomys hatcheri* Wood
a) $M\bar{2}$ right, A.E.W. No. 35-73-11. × 10.
b) $M\bar{1}$ right, A.E.W. No. 35-62-2-3. × 10.
c) $M\underline{1}$ right, A.E.W. No. 35-62-2-3. × 10.
FIG. 35. *Proheteromys nebraskensis* n. sp. Holotype. M.C.Z. No. 5051, $P\bar{4}$–$M\bar{3}$ left. × 10.
FIG. 36. *Proheteromys nebraskensis* n. sp. U. Nebr. No. 45-3-7-33-SP, $P\bar{4}$–$M\bar{1}$ right. × 20.
FIG. 37. *Agnotocastor* sp. indet. Amherst No. 22-551, $P\bar{4}$–$M\bar{3}$ right. × 3⅓.

It is extremely gratifying at last to have both upper and lower teeth of the same species of *Heliscomys*, even if the material is decidedly incomplete.

Range: Middle Oligocene White River Beds of Sioux County, Nebraska, and Washington County, South Dakota.

Heliscomys senex Wood 1935*a*

(Wood, 1935*a*, Fig. 6*a*)

Heliscomys senex Wood, Annals Carn. Mus., Vol. XXIV, 1935.
Holotype: Princeton Univ. No. 13,459, lower jaw with $P\bar{4}$ and $M\bar{2}$–$\bar{3}$ left.

The width of the molars is greater than the length. The cingulum cusps are lower than the cusps of the protomere, and only one is present on $M\bar{3}$. $P\bar{4}$ is formed of three main cusps and two small antero-external ones, one of which is apparently a cingulum cusp, while the other suggests a conulid, although it is probably of different origin. This species is one of the most important of the genus, apparently indicating a stage in the development of a quadritubercular tooth from a tricuspidate one. Several possibilities of the precise mode of this development followed are discussed by Wood (1935*a*, pp. 86–87, 210–211), but as any possible conclusions must be purely tentative, and as no new data have come to light, the discussion need not be reproduced here.

Range: Middle Oligocene Brulé Formation of Slim Buttes, South Dakota.

MEASUREMENTS OF *Heliscomys*

	H. vetus Amer. Mus. Nos. 5461–5462	*H. senex Princeton Univ. No. 13,459*	*H. gregoryi Carn. Mus. No. 10,176*	*H. hatcheri U.S.N.M. 6635*	*H. hatcheri A.E.W. Nos. 35–73–11 ($M\bar{2}$) and 35–68–2–3*
	mm.	mm.	mm.	mm.	mm.
$P\underline{4}$–$M\underline{3}$			3.02		
$P\underline{4}$ a-p			0.85		
width protoloph			0.60		
width metaloph			1.00		
$M\underline{1}$ a-p			0.82		0.79
width protoloph			1.08		0.97
width metaloph			1.04		0.96
$M\underline{2}$ a-p			0.80		
width protoloph			1.02		
width metaloph			1.00		
$M\underline{3}$ a-p			0.55		
width protoloph			0.80		
width metaloph			0.60		
$P\bar{4}$–$M\bar{3}$		3.07			
$P\bar{4}$ a-p	0.48	0.62			
width, anterior		0.37			
width, posterior	0.55	0.56			
$M\bar{1}$ a-p	0.84			0.95	0.93
width metalophid	0.83			0.94	0.89
width hypolophid	0.84			0.89	0.87
$M\bar{2}$ a-p	0.82	0.78		0.89	0.87
width metalophid	0.82	0.92		0.96	0.94
width hypolophid	0.83	0.85		0.86	0.87
$M\bar{3}$ a-p		0.72			
width metalophid		0.69			
width hypolophid		0.54			

Proheteromys Wood 1932

Proheteromys Wood, Florida State Geol. Surv. Bull. 10, 1932.
Genotype: *P. floridanus* Wood, 1932.

"Cheek teeth bilophodont and in about the same stage of development as in *Mookomys*, and likewise based upon a primarily sextitubercular pattern; upper incisors asulcate; heteromyine pattern developing in cheek teeth; $P\bar{4}$ quadritubercular; posterior cingula on lower and anterior cingula on upper teeth." (Wood, 1935*a*, p. 166.)

Range: Upper Oligocene of Nebraska, Lower Miocene of South Dakota, Middle Miocene of Florida and Middle (?) Miocene of Colorado.

Proheteromys nebraskensis sp. nov.

(Figs. 35–36)

Holotype: Mus. Comp. Zoöl. No. 5051, lower jaw with $P\bar{4}$–$M\bar{3}$ left.
Paratype: U.Nebr. No. 45–3–7–33–SP, lower jaw with $P\bar{4}$–$M\bar{1}$ right.

This form is intermediate in size between *P. floridanus* and *P. parvus*. The teeth are proportionately long antero-posteriorly. The posterior cingula are weak. The protostylid of the molars is separate from the cingulum when unworn, and is far to the rear. The protoconid and metaconid are connected by a cingulum along their anterior margins. The cusps are very independent of the lophs, not uniting until the tooth is fully worn. There is an H-pattern in the molars. $M\bar{3}$ has a 2-cusped hypolophid.

It is interesting to note that these specimens, the first heteromyids reported from the Upper White River, definitely belong to a Miocene genus rather than to the typical Oligocene *Heliscomys*. In point of fact, they are extremely close to *Mookomys*, but apparently are referable to *Proheteromys* (and hence to a different subfamily, if we adopt a vertical classification), on the basis of the approach of the two anterior cusps of $P\bar{4}$ to each other, the presence of posterior cingula, and the extremely long cingular crest between the protoconid and the protostylid, which is the first stage in the development of the heteromyine Y-pattern. If, of course, the four cusped type of premolar has been derived from the three cusped in the manner I have suggested elsewhere (Wood, 1935*a*, pp. 86–87, 210–211), then it is quite possible that the approximation of the two anterior cusps in the Heteromyinae and particularly in *Proheteromys* is a primitive character, and that *Mookomys* has been derived, not directly from *Heliscomys* as I had previously suggested, but indirectly, through *Proheteromys*.

P. nebraskensis is more primitive than even the Rosebud form, *P. matthewi*, the individual cusps being more distinct from each other than in that form.

It is interesting to observe that the discovery of these forms puts the break between the primitive heteromyids and the modern subfamilies somewhere in the Oligocene. The specimens of *Heliscomys hatcheri* described above seem to be tending distinctly toward such a form as *Proheteromys nebraskensis*. Further careful collecting in the White River Beds should reveal much of interest in the evolutionary development of these small rodents.

The holotype has a definitely larger premolar than the paratype, and the first molar is also somewhat wider. The posterior cingulum is lacking on $M\bar{1}$ of the holotype. These differences suggest the possibility that these forms might, if better known, represent distinct species. There is, however, no justification for separating them at present.

There is a deep depression between $M\bar{3}$ and the coronoid, but the mandibular foramen was well up on the latter process, and has been broken off in both these specimens. Both jaws are so damaged as to show nothing else of interest.

This species is distinctly larger than its nearest known relative, *P. matthewi*, as may be seen by comparing the accompanying measurements with those given by Wood (1935*a*, Table II).

MEASUREMENTS OF *Proheteromys nebraskensis*

	Holotype, Mus. Comp. Zool. No. 5051	*Paratype, U.Nebr. No. 45-3-7-33-SP*
$P\bar{4}$–$M\bar{3}$	4.63 mm.	— mm.
$P\bar{4}$ antero-posterior	1.02	1.00
width anterior loph	1.02	0.86
width posterior loph	1.11	0.99
$M\bar{1}$ antero-posterior	1.24	1.25
width metalophid	1.38	1.21
width hypolophid	1.42	1.25
$M\bar{2}$ antero-posterior	1.20	—
width metalophid	1.41	—
width hypolophid	1.27	—
$M\bar{3}$ antero-posterior	1.08	—
width metalophid	1.11	—
width hypolophid	0.98	—

Range: Upper Oligocene, Morrill County, Nebraska. The holotype was collected by M. V. Witter, from the *Protoceras* sandstones, Upper Brulé, below the top ash, Jail Rock, Morrill County. The paratype is from the *Leptauchenia* Zone, near Bridgeport, Morrill County, Nebraska.

Family GEOMYIDAE Bonaparte 1850

"The Geomyidae may be described as 'Sciuromorph' rodents with 'skull fossorial; zygoma robust; infraorbital foramen always at end of a long canal, its orifice protected from muscle pressure by counter sinking in an oblique sulcus; frontal without postorbital process' (Miller and Gidley, 1918, pp. 433–434); molars based on a two-lophed, six-cusped pattern, fundamentally identical with that in the Heteromyidae; premolars similar to those in the more advanced forms of heteromyids; cheek teeth progressively hypsodont, usually ever-growing, ultimately with enamel reduced to anterior, posterior, and median plates, or eventually to but a single plate; incisors primitively smooth, progressively develop one or more sulci. *Range:* Middle Oligocene to Recent, of North and Central America." (Wood, 1936 *b*, p. 2.)

The geomyids are practically unknown in the White River, but one specimen having been referred to this family. This is the more surprising in view of the comparative abundance of geomyids (subfamily Entoptychinae) in the overlying Lower Miocene levels of Nebraska, South Dakota and Wyoming, and their extreme abundance in the John Day. With the exception of one poorly known form, all these later groups of fossils fall into the closely related subfamily of the Entoptychinae. The White River form, *Gidleumys*, is

distinctly more primitive than any known member either of the Entoptychinae or the Geomyinae, and, being known from only two teeth, is at present referable to neither subfamily. Nor does it add greatly to our knowledge of the evolution of the family, beyond proving them to have been present in the White River, a fact which would have been obvious anyhow because of their numbers and diversity in the immediately overlying beds.

Gidleumys Wood 1936

(Fig. 39 and Wood, 1936*b*, Fig. 2)

FIG. 39. *Gidleumys adspectans* Wood. Holotype. U. S. Nat. Mus. No. 13,748, P4–M1 left. × 5. After Wood, 1936*b*, Fig. 2.

Gidleumys Wood, Amer. Mus. Novitates No. 866, 1936.
Genotype: *Gidleumys adspectans* Wood, 1936*b*.

The teeth are brachydont, with the cusps still clearly differentiated and the cingulum cusps definitely smaller than the primary ones. P4 bears a strong anterior cingular cusp and has a two-cusped protoloph.

"The premolar of this animal is quite distinctive, in the large basal cusp developed from the anterior cingulum. . . . While this cusp is high and well developed, it is only about half as high as the rest of the crown. The protoloph is formed of two cusps, which seem without question to be the paracone and protocone. This apparently represents an early divergence from some, at least, of the heteromyids, in which the protoloph is reduced to a single cusp. There is no trace of an internal cingulum cusp on the protoloph, which apparently separates it from some at least of the Entoptychines (especially the genus *Entoptychus*), which have three-cusped protolophs. The metaloph is formed of the usual three cusps (metacone, hypocone and entostyle), with a minute accessory cuspule behind the hypocone. M1 is six-cusped, with the crests well developed, but not to the point of obliteration of the individual cusps. The internal cingulum is weak. The teeth of this animal are massive and plump, resembling some of the Miocene heteromyids in general appearance, but differing in the details of the pattern, as well as being an earlier development of the same type of tooth. The latter item seems to have been a universal differentiation between the heteromyids and the geomyids.

"This form unquestionably represents an Oligocene geomyoid. Its large size and progressive character show that it represents a different line from that of its contemporary, the heteromyid *Heliscomys*, though the two are reasonably closely related. As the tooth pattern of *Gidleumys* is what would be expected in a geomyid of this age, it seems reasonable to include it in that family. Due to the apparently excessive development of the anterocone, however, this form does not seem to be an ancestor of the later members of the family, but rather an aberrant side line, which cannot with safety be referred to either of the subfamilies. Some species of entoptychines possess an anterior cingulum but none show any trace of an anterocone except in the milk premolar. Three lophs are also present

on the milk teeth of recent geomyids. . . . There is, however, too little difference in wear between the premolar and the molar to permit the tooth in *Gidleumys* to be a milk tooth. Although the anterocone might have been secondarily reduced in later forms, it seems more probable that this animal represents an aberrant and otherwise unknown line." (Wood, 1936*b*, pp. 3–4.)

Gidleumys adspectans Wood 1936

Gidleumys adspectans Wood, Amer. Mus. Novitates No. 866, 1936.
Holotype: U.S.N.M. No. 13,748, fragment of the left maxilla with P4–M1.
Range: Middle Oligocene White River of South Dakota.

Superfamily **CASTOROIDEA** Gill

It is difficult at the present time to make a satisfactory definition of this superfamily. It has generally been considered to contain only the one family, the Castoridae. I am, however, referring the Eutypomyidae to the same group. It is impossible to determine at present the correct relationships of these rodents, either with each other or with any other members of the order. On the one hand, there are many striking similarities to the other "Sciuromorphs," so that for the present, at least, I have left them with this suborder. Of these the most important is the zygomasseteric pattern. On the other hand, there are striking similarities between the tooth pattern of the beavers and that of certain porcupines. This is so marked in some forms that the Pleistocene *Castoroides* has frequently been placed with *Amblyrhiza*, on this account alone. Of course, since this similarity is between end members of the two lines, it should not be too heavily emphasized. But the elucidation of the relationships of the castoroids is not rendered any more certain by the entire absence of fossils sufficiently primitive to give any indication as to what their ancestral tooth pattern might have been.

Family Castoridae Gray 1821

Miller and Gidley (1918, p. 435) define this family as follows: "Skull with rostrum broadened and deepened and braincase narrowed; basioccipital region with conspicuous pit-like depression; cheekteeth not evergrowing but so excessively hypsodont [in later forms] that the . . . pattern . . . changes little with age and rarely if ever wears out. . . ." The primary habitus is fossorial, with a later aquatic one superposed on it.

Range: Lower Oligocene to Recent of the northern continents.

The earliest well known beavers are those of the Lower Miocene. While there are a number of specimens known, from several levels in the Oligocene, the specimens are in such poor condition that little can be told of their tooth patterns. This means that any attempt at working out their relationships must be pure guess-work. I make this statement advisedly, in spite of the general assumption to the contrary. Stirton (1935, chart 2) shows the beavers as probably descended from *Paramys*. Taylor (1915) sums up the standard opinion by saying "The genera, *Paramys* (Eocene), *Sciuravus* (Eocene), and *Steneofiber* (Oligocene and Miocene), are near, if not actually, members of the phylogenetic series, of which the genus *Castor* is the latest development." It is, of course, probably unnecessary to point out that species correctly referred to *Paramys* could by no stretch of the imagination be ancestral to *Sciuravus*, and that there is absolutely no evidence that the latter is ancestral to the beavers. In fact, as indicated above, except for the aberrant

genus *Eutypomys*, I know of no forms that seem at all close to the Castoridae. They are still, as they were in the time of Coues and Gill, one of the most isolated of the rodent groups. The elucidation of rodent relationships has not been helped by the facile assumption that the relationship between the Sciuridae and the Castoridae has been proved.

Agnotocastor Stirton 1935

(Pl. XXVIII, Figs. 1, 1*a*, 1*b*)

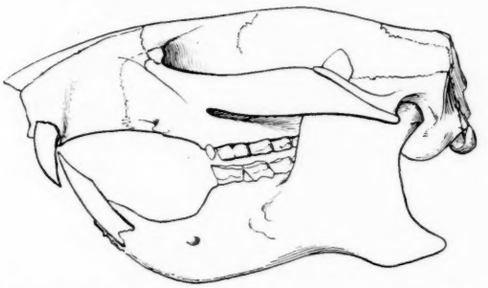

FIG. C. Skull and Jaws of *Agnotocastor*. Approximately natural size.

Agnotocastor Stirton, Univ. Calif. Publ., Bull. Dept. Geol. Sci., Vol. 23, No. 13, 1935. Genotype: *A. praetereadens* Stirton, 1935.

"Rostrum long and narrow; skull relatively narrower than in *Palaeocastor;* hypostria shallow; no canal piercing basioccipital at end of basispheno-basioccipital groove; bulla apparently kidney-shaped; dental formula I$\frac{1}{1}$, C$\frac{0}{0}$, P$\frac{3}{3}$–$\frac{4}{4}$, M$\frac{1}{1}$–$\frac{3}{3}$; alveoli for incisor round (but I cannot tell whether the anterior surface of the incisor was convex as in *Eucastor* and *Steneofiber* or flat as in *Palaeocastor*); P$\frac{3}{3}$ represented by small alveoli; cheek teeth apparently lower crowned than in *Palaeocastor;* P$\frac{4}{4}$ nearly square in outline; molars nearly rectangular in shape, elongate transversely; enamel borders of fossettes and flexi thicker than in *Palaeocastor;* fossettes and flexi wider than in *Palaeocastor;* mesostria and hypostria of equal or nearly equal length; two fossettes anterior to the mesostria in a late stage of wear." (Stirton, 1935, p. 395.)

Range: Lower, Middle and Upper Oligocene of Wyoming, South Dakota and Montana.

The upper teeth are those of a typical beaver, and are tantalizingly useless in determining a source from which the beavers could be derived. The arrangement of the lakes (Pl. XXVIII, Fig. 1*b*) is almost exactly the same as in *Palaeocastor*. The reduction of the molars and enlargement of the premolar seen in later beavers has already taken place. The teeth are mesodont, rather than hypsodont as in *Palaeocastor*. There is no evidence of the complexities of pattern that occur in *Eutypomys*. It would seem, however, that the protocone and hypocone (separated by a strong hypostria) are fully developed. The protocone is continued directly into an anterior cingulum which may have ended in a parastyle, but, at any rate, was united with the paracone. This latter was indirectly connected with the protocone by a weak crest, fundamentally as in *Eutypomys*. The posterior part of the outer surface of the tooth consists of two portions, interpreted by Stirton (1935, Fig. 4) as mesostyle and metacone respectively, but which I would prefer to interpret as metacone and metastyle. There are two small lakes in this lobe in Amer. Mus. No. 1428, the diplotype, which suggests that this lobe may represent the mesostyle, metacone and metastyle.

If my interpretation is correct, *Agnotocastor* and all later members of the Castoridae are notable for their entire lack of a complete metaloph, the metacone and hypocone being connected only via the posterior cingulum. There is, of course, no question but that the connection is through the posterior margin of the tooth. This condition is quite different from that seen in *Eutypomys*, where the metaloph is clearly and unmistakeably complete (see below, Fig. 40), and is unusual, to say the least.

The molars have a pattern similar to the premolar, but show a distinct antero-posterior compression. This is least marked on M3, which likewise shows some details of the pattern in the only available specimen. In this tooth, the metacone and metastyle seem to have been separate, strengthening the interpretation I have given of the cusp relations in the premolar. The posterior fold of M3 certainly is not the metacone. The teeth are proportionately as large as in *Palaeocastor*.

The closest resemblances of the skull are to *Eutypomys* and *Palaeocastor*, especially the former, though the skull of *Agnotocastor* is intermediate between the other two. All three had skulls of about the same actual length, but that of *Eutypomys* is narrow, *Palaeocastor* broad and fossorial, and *Agnotocastor* intermediate. The incisors seem to have extended beyond the nasals as in *Palaeocastor*, rather than the reverse as in *Eutypomys* and *Ischyromys*. The temporal crest begins with the lachrymal tuberosity as in *Eutypomys* rather than continuing the dorsal edge of the zygoma as in *Palaeocastor* and later beavers. The crests unite just behind the narrow point of the postorbital constriction, as in *Palaeocastor* and *Eutypomys*. This point is distinctly further anterad than in *Eutypomys*, and is about in the same relative position as in *Palaeocastor*. The eye was small and apparently directed upwards, as in *Palaeocastor*, instead of being large and looking outward as in *Eutypomys*. The nasals end in front of the infra-orbital foramen, being shorter than in *Palaeocastor*. They are continued to the temporal crests by a flat area of the frontals that has every appearance of being a part of the nasals, but really is not. The parietals have the same anterior invagination found in *Ischyromys* and *Palaeocastor* (Peterson, 1906, Pl. XVII, Fig. 2). The frontal does not extend as far caudad in any of these forms as it does in *Eutypomys*. The braincase is broad and flat, more so than in any other White River rodent except perhaps *Cylindrodon*. It is longer than in *Palaeocastor*, and much narrower. In *Palaeocastor*, the transverse diameter of the braincase is, if anything, greater than the antero-posterior. In *Agnotocastor*, the antero-posterior is distinctly greater than the transverse. The occiput is visible in dorsal view, though not as much so as in *Palaeocastor* and later beavers. The interparietal is long and narrow, as in *Palaeocastor*, rather than short and broad as in *Eutypomys* and *Ischyromys*. It is not triangular as in *Palaeocastor*, however, but the sides are parallel for most of its length, and the bone then tapers suddenly to a point at the anterior end. The temporal foramen is small as in *Palaeocastor*, thus differing from *Eutypomys* and *Ischyromys*, which have large openings.

As the only available skull (Amer. Mus. No. 1428) is crushed vertically, the lateral aspect is particularly subject to misinterpretation. The frontal region is high, in part at least due to distortion. There seems, nevertheless, to have been an arching of the skull over the cerebrum and a depression over the cerebellum, as in *Ischyromys*, contrasting with the even upper surface in *Eutypomys* and *Palaeocastor*. This suggests the possibility that the brain of *Agnotocastor* was smooth as in *Ischyromys*, while that of *Palaeocastor* was convoluted as in *Eutypomys*. The evidence, however, is entirely inadequate on this point.

The rostrum is very much more slender than in *Eutypomys*, and distinctly more so than in *Ischyromys* or *Palaeocastor*. The maxillary root of the zygoma was further forward than in *Eutypomys* or *Ischyromys*, having already developed typical beaver relationships in this respect. Also typical of the beavers, in contrast with *Eutypomys*, is the heavy tuberosity for the masseter below and laterad of the infra-orbital foramen. This is proportionately as large as in the recent beaver, and, in view of its complete absence in other phyla of "Sciuromorphs" adds to the evidence for the early specialization of the various lines of rodents. The infra-orbital foramen is much smaller than in *Eutypomys*, being more nearly round, instead of being elongate dorso-ventrally, in which respect it resembles *Palaeocastor*.

The maxillo-premaxillary suture passes to the rear of the incisive foramen, instead of through its middle as in *Palaeocastor*. The foramen is entirely anterad of the level of the infra-orbital foramen, as in *Eutypomys* and *Ischyromys*, instead of being level with it, as in *Palaeocastor*. These are primitive characters, and merely indicate an absence of beaver specializations. The space between the infra-orbital foramen and the zygoma was narrow. The palate is narrow as in *Palaeocastor*, but smooth as in *Ischyromys* and *Eutypomys*. It presents a specialization in its narrowness, but is still primitive in its smoothness. The bullae are badly damaged, but the external auditory meatus seems to have been at the postero-dorsal angle of the bulla and to have opened upward, as in *Palaeocastor*. The paroccipital processes are larger than in this form, and extend almost as far caudad as do the condyles. These are quite different in shape from those of *Palaeocastor*, having large ventral portions that almost meet in the midline. The mastoid forms a much more considerable section of the occiput than in *Palaeocastor*. The foramen magnum is of typical beaver shape, being a somewhat rounded triangle.

An interpretation of the characters of the skull of *Agnotocastor* leads us to the conclusion that this animal was already beginning to adopt the burrowing habitus which became so strongly imposed on the Miocene beavers, and which has become the fundamental heritage of the recent members of the family. The short nasals, flattened skull, broad braincase, the small eye, situated high on the head and looking upward rather than outward, the dorsal opening of the auditory meatus, all suggest that this animal was already becoming adapted to a fossorial form of life. The hypsodonty of the cheek-teeth would then be an adaptation to the wear of the teeth resulting from the sand which the animal would of necessity get into his mouth while burrowing.

A pair of lower jaws, Amherst No. 22–551, from the *Titanotherium* Beds of Indian Creek, Wyoming, are tentatively referred to this genus (Fig. 37). The teeth are so badly worn that the reference is somewhat uncertain. From what little remains of the pattern, however, it appears to resemble what the lowers of *Agnotocastor* must have been. This animal certainly was neither *Ischyromys*, *Titanotheriomys*, *Sespemys* nor *Eutypomys*, and hence must represent either an *Agnotocastor* or an otherwise unknown form. The mandible is much more suggestive of *Eutypomys* than of *Palaeocastor*, the shape of the jaw, of the masseteric fossa, the position of the mental foramen, and the size and shape of the knob for the incisor, all resembling conditions in the former. The incisor is much heavier than in *Eutypomys*, suggesting that of *Palaeocastor*, but the anterior face is rounded, instead of being flat as in the Miocene form, thus fitting into Stirton's second main division of the beavers (1935, p. 395). In $P\overline{4}$, the only tooth to retain any lakes, they are arranged in a

manner similar to that of *Palaeocastor*, and quite different from that of any other Oligocene rodent.

Thus, while the evidence as to the pre-Miocene history of the beavers is still exceedingly scanty, the family seems already to have been well established in the Oligocene, with the typical beaver tooth pattern and the typical beaver infra-orbital foramen. The lower jaws from the *Titanotherium* Beds, if correctly identified, show that we cannot hope to find an Oligocene ancestor of the Castoridae, but that we must look for such a thing in the Eocene. The complete development of the beaver zygomasseteric structure and of the beaver tooth pattern by the Oligocene suggests a considerable antecedent period of evolution along pre-beaver lines. The entire absence of rodents other than Ischyromyoids from American deposits earlier than uppermost Eocene suggests that either the Eocene evolution of the "Sciuromorphs" took place in a region whose fossils are not yet known, or that we merely have not found the ancestral forms yet, or that there were no rodents other than Ischyromyoids in the Middle Eocene. This last hypothesis strikes me as being exceedingly improbable in view of the already high specialization of the earliest known rodents, indicating a long pre-Eocene ancestry for the group, and of the fact that the difference between the Middle Eocene Ischyromyoids and such Oligocene "Sciuromorphs" as *Agnotocastor* and *Eutypomys* is greater than between these Oligocene genera and their recent relatives. Matthew and Granger (1925, p. 7) suggest that *Ardynomys* might have been ancestral to "*Palaeocastor* of the Upper Oligocene." This seems to have been an entirely mistaken suggestion, all the present evidence being that *Ardynomys* was related to *Cylindrodon* and ancestral to *Tsaganomys* and *Cyclomylus*, and that it could have had nothing to do with the line of the beavers, *Ardynomys* and all its relatives being typical Ischyromyoids of a high degree of specialization.

Agnotocastor praetereadens Stirton

Steneofiber nebrascensis (Leidy), Matthew 1902 (nec *S. nebrascensis* (Leidy), = *Palaeocastor nebrascensis* Leidy 1856).

Agnotocastor praetereadens Stirton, 1935.

Holotype: Amer. Mus. No. 1428, a partially crushed skull without zygomata or incisors, from the *Protoceras* Beds on the Cheyenne River, South Dakota.

The diagnosis of this form is the same as that of the genus.

Another specimen, a partial skull with P4–M2, was originally associated with the holotype, but has been exchanged with Dr. Beaufort, of Amsterdam, Holland.

? **Agnotocastor montanus** (Scott)

Steneofiber montanus Scott, 1893.

?*Agnotocastor montanus* (Scott), Stirton 1935.

This species, from the Miocene of Montana, was represented only by the holotype, now lost. It agrees with *Agnotocastor*, however, in the enlargement of P4, the antero-posterior compression of M1, and the general appearance of the fossettes and flexi (Stirton, 1935, p. 396). "In both of the lower teeth represented in the specimen, the antero-posterior diameter of the crown exceeds the transverse, which is very unusual for this genus. The incisors are narrow, with anterior faces which are less convex than in *Castor*, and are covered with a thick layer of orange-colored enamel." (Stirton, op. cit., p. 397.)

? **Agnotocastor** sp. indet.

The lower jaws discussed above (Amherst No. 22–551) agree with ?*Agnotocastor montanus* in a number of respects. The antero-posterior diameter of the lower molars is greater than the transverse (Fig. 37). The lower incisors are rounded, and with a strong coating of orange enamel. It is probable, however, that when better known, this form will be seen to be at least specifically distinct from ?*A. montanus*.

Castorid, gen. indet.

Stirton (1935, p. 396) mentions a castorid (Univ. Cal. No. 30570) from the Oreodon Beds which he discusses under *Agnotocastor praetereadens*. In view of the fact that this specimen has flat incisors whereas the type of *Agnotocastor* almost certainly had round incisors, it is probable that this specimen is the only known Oligocene representative of the flat-incisored *Palaeocastor* line. As Stirton says, however, "this specimen alone is too poorly preserved and its characters are too uncertain for it to be considered the type of another genus. . . . It is possible . . . that they may represent distinct genera, *Agnotocastor* being in the line of ancestry of *Eucastor* and related forms, whereas No. 30570 may be the Oligocene predecessor of *Palaeocastor*. At present these questions cannot be answered." (Op. cit., p. 396.) While this last statement of Stirton's is indubitably correct, the material is very suggestive of two lines of beavers being present at least as far back as the Middle Oligocene.

Eutypomyidae Miller and Gidley

Miller and Gidley (1918, p. 435) defined this family as follows: "Like the Adjidaumidae but with cheekteeth somewhat more hypsodont and the heptamerous enamel pattern complicated by the development of a considerable number of secondary closed loops which appear in partially worn teeth as an aggregation of minute enamel lakes covering nearly entire surface of crown." This definition appears to be inadequate or incorrect in a number of particulars. The pattern does not seem to be based on seven cusps, neither is it similar in fundamentals to that of the adjidaumids (= eomyids). The cusp between the paracone and metacone seems to be a mesostyle, rather than a mesocone as in eomyids. There does not seem to be any indication of proto- and metastyles, which would be required to give a true heptamerous pattern. The relations seem to be with the Castoridae rather than with any other "Sciuromorphs."

Perhaps a better definition of the family would be: primitive castoroids, with a primitive skull, squirrel-like except for the entire absence of postorbital processes. The auditory meatus was directed posterad. The dental formula was $P\frac{2}{1}$, $M\frac{3}{1}$, the pattern being based on four main cusps with connecting crests.

Range: Lower to Middle Oligocene of Saskatchewan, Montana, South Dakota and Nebraska, only one genus being known.

Eutypomys Matthew

(Pls. XXIX and XXX and Pl. XXXI, Figs. 1–2)

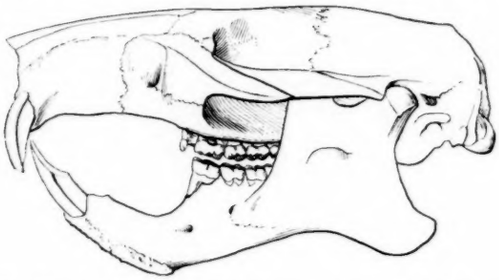

FIG. D. Skull and jaws of *Eutypomys*. Approximately natural size.

Genotype: *E. thomsoni* Matthew, 1905, from the Oreodon Beds of South Dakota.

This is a relatively primitive castoroid with extremely complicated enamel folds on the cheek-teeth. The eye is large and directed forward and outward, while the ear is small, directed upward and backward. The jaw is slender, and the condyle far to the rear. The outer border of the pes is much strengthened, though all five toes are subequal in length. The navicular is extremely short. The proximal ends of the metatarsals interlock in a striking fashion, which I have seen elsewhere only among the Geomyidae. The two inner toes are very slender.

The cheek-teeth are medium-crowned, being distinctly higher than in *Ischyromys*, but very definitely and clearly rooted as soon as erupted. The crown does not extend into the alveolus of fully erupted teeth. The teeth are extremely complicated in pattern, although there is much more visible pattern in the arrangement of the lakes than is indicated by Matthew's figure of the teeth (1905, Fig. 2).

Although the third upper premolar is very small, it nevertheless shows some complexities of pattern. It is formed, primarily, of a single main cusp, with a main U-shaped elevation around the top, and several subsidiary rugosities (Fig. 40). This tooth seems to have been of little functional importance, there being no evidence of its having suffered any wear in the diplotype. In Amherst No. 20–187, however, it is considerably worn.

$P\underline{4}$ shows the fundamental pattern better than any of the other teeth of Matthew's specimen. The paracone, metacone, protocone and hypocone may be clearly distinguished, connected in pairs to form protoloph and metaloph. The widely separated protocone and hypocone are connected by a diagonal mure. The mesocone seems fairly well developed in this tooth, but the mesoloph seems almost entirely absent. The area that should be occupied by the mesostyle is filled with a complex of three or four small crests. The rest of the central valley has been invaded by irregular outgrowths from the protoloph and metaloph and from the mesocone. There is no clear indication of conules. In fact, more evidence could be adduced for the presence of two or three in each loph than of one. The posterior cingulum is normal, except for the multiplicity of its secondary connections with the metaloph. The anterior cingulum unites with the center of the protoloph in such a way as to suggest that the point at which it meets the loph still represents the anterior arm of the protocone. If this should be the case, there is clearly no protoconule. However, in view of the close proximity of the lingual end of the cingulum to the protocone,

and of the conditions visible in the molars, it is very possible that this union is secondary, and that the primitive one is via the lingual end of the cingulum.

The patterns of the first two molars seem identical, in their main features, with that of P4. The anterior cingulum seems slenderer in these forms, and more certainly to have

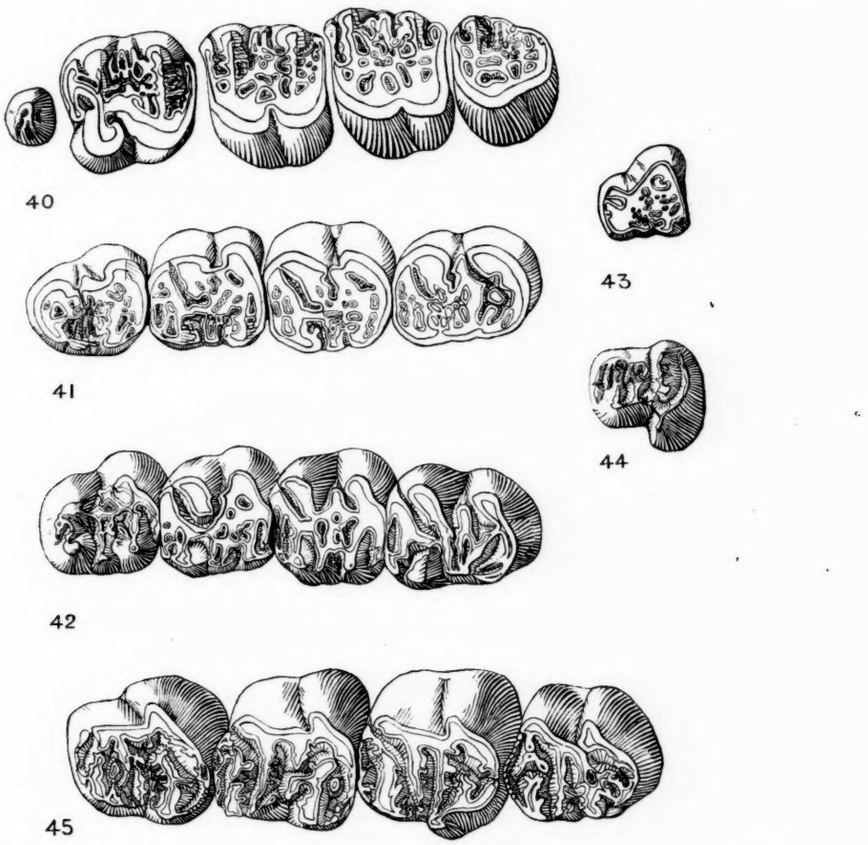

FIG. 40. *Eutypomys thomsoni* Matthew. Holotype. Amer. Mus. No. 12,254, P3–M3 left.
FIG. 41. *Eutypomys thomsoni* Matthew. Holotype. Amer. Mus. No. 12,254, P4–M3 right.
FIG. 42. *Eutypomys thomsoni* Matthew. M.C.Z. No. 6191, P4–M3 right.
FIG. 43. *Eutypomys parvus* Lambe. Holotype. Can. Nat. Mus. No. 6482, P4 right.
FIG. 44. *Eutypomys* sp. Specimen from Thompson Creek Beds, Montana. P4 left.
FIG. 45. *Eutypomys magnus* n. sp. Holotype. Princeton Univ. No. 13,779, P4–M3 right.
All figs. × 5.

united directly with the protocone. The mesocone is less clearly indicated. M3 is considerably smaller than are the other teeth, although in Amherst No. 20–187 it is considerably larger than in any other known specimen. This tooth appears to have suffered particularly reduction of the metacone, which is barely distinguishable. In Amer. Mus. No. 1423, from the Lower Oreodon Beds, the hypocone of M3 is very poorly developed. There thus seems to have been considerable variation in this tooth. In all of the molariform teeth, the paracone and half of the protoloph stand up above the rest of the tooth as a ridge. This is also true of the metacone and part of the metaloph, except in M3.

The lower teeth show their fundamental pattern just as clearly as do the uppers. In $P\overline{4}$, two main anterior cusps, connected via their anterior ends, and perhaps also posteriorly, are clearly visible. The mesoconid is large, and the hypoconid and entoconid are connected directly by a crest, as well as indirectly through the posterolophid. A fair sized central basin is shown (Figs. 41–42), although it is much reduced and is invaded by numerous minor folds of enamel. The molars show a rather different pattern. The protoconid is widely separated from the metaconid, never uniting directly with it, and joining the anterior cingulum only after considerable wear. The mesoconid is much smaller than in the premolar. The central basin, however, seems completely to have disappeared, being filled by the complicated mesostylid which connects with both metaconid and entoconid. The posterior half of the two anterior molars seems similar to that of $P\overline{4}$. In $M\overline{3}$, the entoconid is small and unites with the hypoconid only through the posterolophid, though a direct union would probably be effected after further wear. In all the molars, the hypoconid and mesoconid are distinctly separated, the ectolophid being poorly developed.

The tooth pattern, particularly that of the lower teeth, is reminiscent of that of certain late Miocene beavers, as *Amblycastor tungurensis* Stirton (Stirton, 1935, Figs. 53–59). The similarity is very suggestive of that between the heteromyids and the geomyids. For that reason, and in view of the numerous similarities in the skull between *Eutypomys* and the beavers, discussed below, I have tentatively referred the Eutypomyidae to the Castoroidea.

One of the closest analogies in tooth pattern that I have seen to that of *Eutypomys* occurs in *Paramys sensu strictu* (i.e., in the Bridger species). Here there is a similar development of complex wrinkles in the enamel, although they do not become so prominent a part of the pattern. In the upper molars, this similarity reaches such a point that it is almost suggestive of genetic relationships. The lower molars, however, clearly show that this resemblance is merely parallelism, since the protoconid and hypoconid in *Paramys* are connected by a continuous ectolophid, while in *Eutypomys* there is a distinct transverse valley at this point, clearly seen in little worn teeth. Even aside from this, it seems impossible to match the details of the patterns in the lower teeth of the two genera, and it is necessary to assume that the similar types of patterns are entire parallelisms. The same is true of the similarity in pattern to *Amblycastor*, noted above. It should be remembered, however, that by and large, the greater the parallelism between any two forms, the closer is their relationship.

There is, as will be clear from the above, little if any resemblance between the teeth of *Eutypomys* and those of contemporary castorids, other than the resemblances which unite most rodents with each other, the resemblances of *Eutypomys* to beavers being to the later and more specialized members of the family.

As is natural in a form with such extravagant complications of the pattern, there is a great deal of individual variation in the details, these often varying to a considerable amount on the two sides of the same individual. At present, it is impossible to determine any specific characters in the teeth, and I have based the three species that I recognize merely on clear differences of size.

The anterior face of the lower incisor is rounded, the enamel extending over half the tooth, when seen in side view, instead of ending near the front of the tooth, as in the beavers. The upper incisors have a flat anterior face, with the normal distribution of the enamel, as is shown in Matthew's figure (1905, Fig. 1), and in Pl. XXIX.

The *skull* is that of a typical primitive "Sciuromorph." The infra-orbital foramen is well forward and high on the face, separated from the zygoma by a broad surface filled, in life, by the *masseter lateralis*. The muscle extended slightly above and anterad of the foramen, beginning at the alveolar border by P$\underline{4}$. There is a slight thickening of the lateral border of the foramen, separating it from the muscle. This is very weak, as in some squirrels, and there is no trace of the crest or knob which occurs in beavers and the larger squirrels. The general shape of the skull—long and relatively slender, with a small braincase—is that of primitive rodents in general. There is no trace of the postorbital processes so characteristic of the Sciuridae. There is no sign of the transversely inflated braincase of the beavers, nor of the swollen brain of the squirrels. The braincase is sufficiently small so that the temporal crests have no difficulty in uniting to form a sagittal crest just behind the orbits. Anteriorly, the temporal crests end in a small process extending over the anterior part of the orbit. The zygomatic branch of the maxilla is extended downward as in beavers (Peterson, 1906, Pl. XVII, Fig. 1), and has a long contact with the malar, which bone is missing in all known specimens of *Eutypomys*. It seems, however, as if this region may have been similar to that in *Palaeocastor*. The palate is broader than in beavers, and ends by the anterior end of M$\underline{3}$, instead of behind the molars, as is the case in *Palaeocastor*. The incisors are more procumbent than in either beavers or squirrels. The zygoma is proportionately heavier than in squirrels. The premaxillary-maxillary suture is more nearly vertical, and the maxillary extends much higher into the orbit than in squirrels. The optic foramen is much smaller, and the foramen lacerum anterius the same size, as in squirrels. There is a large temporal foramen, similar to that in *Palaeocastor*, and larger than I have seen in any squirrels. The bullae are much less inflated than in sciurids, but otherwise similar, especially to marmots. The paroccipital and mastoid processes are on the same transverse line, quite different from *Sciurus*.

The cerebral hemispheres differ strikingly from those of *Ischyromys*, being very short and broad, and actually wider than long. There is a distinct suture near the midline, and a few others, less distinct. Laterally, the brain is quite smooth (Pl. XXXI, Fig. 2). This seems to have been an intellectually much higher form than *Ischyromys*.

The *lower jaw* is much longer and more slender than was indicated by Matthew's figure (Matthew, 1905, Fig. 1), being about the shape and proportions of the jaw of *Sciurus*. The coronoid (Pl. XXIX, Fig. 1) rises gently from the body, and is distinctly smaller than Matthew indicated, apparently resembling that of *Sciurus*. The notch between the coronoid and condyloid processes is also squirrel-like. The condyle is higher than in squirrels, and extends well out to the rear of the jaw, with a head elongate antero-posteriorly. At the same time, the articular surface extends well onto the lateral side of the bone, thus differing from all sciurids with which I have compared it. The base of the incisor makes a large knob on the lateral surface of the ascending ramus, separated from the condyle by a deep fossa, a character seen in no sciurids. Such a knob, however, does occur in *Palaeocastor* and *Agnotocastor*. The position, shape and size of the angle seems to have been much as in sciurids. The masseteric fossa rises much less abruptly than it appears from Matthew's figure. The fossa differs from that of *Sciurus* chiefly in ending slightly further posterad, a character of little significance, and in its development of irregularities, the fossa being smooth in sciurids. The mental foramen is beneath the anterior end of P$\overline{4}$, rather than under the middle of the diastema as in *Sciurus*, *Marmota* and *Cynomys*. The region

below the symphysis shows a great number of fine rugosities in the diplotype, which are probably a sexual character, as they are much less emphasized in other specimens. I have not, however, seen them so well developed in any other rodents. They occur, to a lesser degree, in *Marmota*. There is a very deep pit on the lingual side of the jaw, just posterad of the symphysis, which seems to have served as the origin of either the geniohyoid, or, less probably, of the geniohyoglossus. A faint trace of such a pit is seen in sciurids. In cricetids, the general area is demarcated as a fossa, though there is no sharply limited pit as in either *Eutypomys* or the sciurids. It is also indicated in *Ischyromys*. In general, the lingual face of the jaw is almost identical with that of *Sciurus*. In particular, the mandibular foramen is almost identical in position and relationships in both forms, being a deeply buried opening, high on the ascending ramus (Pl. XXXI, Fig. 1).

The general similarity of the vertebrae to those of *Sciurus* is quite striking. This shows up least of all in the axis, which is like that of *Palaeocastor* (Peterson, 1906, Pl. 18, Figs. 9, 9*a*, 9*b*), but widely different from that of both *Castor* and *Sciurus*, the vertebrarterial foramen being smaller and closer under the zygapophyses than in either of the recent genera. There is a strong mesio-ventral crest, not present in *Sciurus*. There is no trace of the paired foramina seen on the dorsal and ventral surfaces of the centrum of *Sciurus*. The odontoid process has a distinct knob on the dorsal surface, not present either in *Sciurus* or in *Palaeocastor*.

In the holotype of *E. thomsoni*, the sixth and seventh cervicals, the first, fourth, fifth, seventh, eighth and ninth dorsals are preserved. All of these possess large paired foramina on the dorsal surface of their centra as in *Sciurus*. There seems to be no similarity to the vertebrae of *Castor*. In the sixth and seventh cervicals, there are also paired foramina on the ventral surface, thus differing from *Sciurus*, in which the ventral foramina are not paired anterior to the lumbars. The inferior portion of the transverse process of C6, while broken, seems much larger than in *Sciurus*. On the seventh, eighth and ninth dorsals, there is a large fossa between the tubercular facet and the transverse process above it, as in squirrels (Pl. XXX, Figs. 7–9).

The *ribs* show little of great significance, seeming to be similar both to those of *Sciurus* and to those of the beaver.

In most of the preceding comparisons, the similarity is with sciurids rather than with castorids. The *scapula*, however, is much more like that of a beaver than like that of a squirrel, although it is closer to that of *Castor* than to that of *Palaeocastor*. The glenoid fossa is rounder than in *Sciurus*, approaching the beaver in this respect. The coracoid process differs from that of the beaver in being heavier and much shorter. In this respect, it is even more different from that of *Sciurus* and *Palaeocastor*. The groove between the coracoid and the glenoid is much deeper in *Eutypomys* than in any of the others.

The *humerus* is generally similar in *Eutypomys* to that of *Paramys*, *Ischyromys*, and *Sciurus*, being long and slender, instead of short and massive as in *Palaeocastor*. There is no appreciable distinction in the size of this bone between *Eutypomys* and *Ischyromys*. The distal end is heavier in the former, especially the entepicondyle and the supinator crest. The deltoid crest is much heavier in *Eutypomys* than in *Paramys*, *Ischyromys* or *Marmota*, ending distally in a strong rugosity. It is, however, much higher on the bone than in *Palaeocastor*, and shows none of the hypertrophy seen in that genus. The supinator crest is much smaller than in *Palaeocastor*, and resembles that of *Paramys* or *Sciurus*.

The lesser tuberosity is poorly distinguished, the bicipital groove being shallow, again distinguishing *Eutypomys* from *Palaeocastor*.

The fragment of the distal end of the *tibia* that is preserved shows little of the character of the shaft. The internal malleolus is heavy. The fibula was entirely separate. The most striking feature of the bone is the long posterior process (Pl. XXX, Fig. 5), which very definitely limits the freedom of movement of the tibia over the astragalus, and prevents the backward rotation of the former to a vertical position. This process is much more mesiad than in *Ischyromys*, occupying about the same position as in *Paramys*. It is, however, distinctly longer and more twisted than in that form, the groove for the tendon of Achilles extending much more mesiad. In *Paramys*, this process and the medial malleolus are of about the same length. In *Eutypomys*, however, the process is much longer than the malleolus. The proximal end of the tibia, which is associated with Amer. Mus. No. 12,254, is much more like that of *Paramys* than like that of *Ischyromys* or *Sciurus*. The lateral fossa is deeper, proportionately, than in *Paramys*. The sides do not narrow as rapidly as in *Ischyromys*, being about as in *Paramys*. The medial condyle seems to have been the larger, a distinction from *Ischyromys*, though not as much larger as in *Paramys*, and appears to have been very similar to that of *Sciurus*. There is a strong crest dividing the posterior fossa into two parts, which is present neither in *Ischyromys* nor *Paramys*. The shaft of the bone seems distinctly curved, differing from *Paramys* but suggesting *Ischyromys*. The shaft is not curved in the same manner as in *Palaeocastor*, nor is the posterior hook of the distal end at all alike in the two genera. In fact, there seems to be no basis for a close comparison between the tibia of these two forms.

Matthew's figure of the *pes* is quite inaccurate. He shows (1905, Fig. 3) the calcaneum and the cuboid not fully articulated, so that the foot is flat. Actually, the calcaneum was bent upward, making a distinct angle between it and the astragalus, on the one hand, and the rest of the foot, on the other (Pl. XXX, Fig. 2*a*). The distal face of the calcaneum slopes away from the toes, while the cuboid is also wedge shaped, forcing the heel upwards. Either the mesocuneiform has been lost since Matthew described the form, or the bone he figures as such is really the proximal and somewhat broken end of metatarsal II. The navicular must have been very short, as there is only a very small space available for it between the astragalus and the ectocuneiform. This last is short and broad, much shorter proportionately than in *Paramys*. The cuboid is similar, in dorsal view, in the two genera. The bone Matthew figured as the distal end of metatarsal II seems, from its diameter, to belong rather to metatarsal I, having about the same area in cross section, and being much more slender than the preserved portion of the shaft of metatarsal II. Metatarsals III–V have a highly developed interlocking series of knobs and basins (Pl. XXX, Fig. 2), similar to that which is found in recent geomyids. I can recall having seen such interlockings nowhere else in the order. The rest of the foot, however, is entirely different from that of gophers, and rather resembles *Sciurus*, which has no traces of the interlockings. Traces of similar interlockings occur on metatarsals I and II, though they are nowhere near as highly developed. The distal end of metatarsal III is broken, though only the epiphysis is missing, as may be told from the slight swelling of the most distal part of the bone that is preserved. There is no evidence that metatarsals IV and V were longer than III, as Matthew showed them, and it seems intrinsically probable that they were somewhat shorter. The peculiar appearance of the distal end of metatarsal V is due to its having

been crushed. It would seem that only a short section of the middle of this bone has been lost, instead of the longer section indicated by Matthew's figure. There is a remarkably strong median ventral keel at the distal end of this bone. There must have been a similar keel on the fourth metatarsal, as may be told from the groove to receive it in the proximal phalanx. In the third digit, this keel seems to have been of more normal size, the groove of the phalanx being shallower. These keels are very similar to those in the corresponding position in the cat, and seem to indicate a corresponding flexion of the foot at the distal ends of the metatarsals, especially well developed at the lateral margin. Metatarsal V could not have touched the cuboid, as Matthew thought it did, differing in this from *Palaeocastor*, where the two bones just meet. The hallux was remarkably long and slender, metatarsal I being nearly as long as III. The second is heavier than the first, but still seems quite slender when compared with the three lateral metatarsals. As Matthew indicated, the hallux diverges. The second digit seems to have done the same, though to a lesser degree. There could not, however, have been any opposability of the hallux, movement between the metatarsal and the entocuneiform being almost non-existent, and what little there was apparently being limited to a vertical plane. The whole outer part of the foot was strong and closely knit together. The proximal end of the medial phalanx of digit three shows an almost flat surface, suggesting that there was very little movement between the medial and proximal phalanges. The articulation of the medial and ungual ones was more normal.

Whatever the resemblances to *Castor* (and they are not very striking), there seems to be no similarity to the pes of *Palaeocastor fossor* (Peterson, 1906, Pl. XVIII, Fig. 14). In this form, the axis of symmetry passes through the third digit, the fifth is short, the second is as stout as the fourth and third, the first is short, the first two do not diverge, the joint between the proximal and medial phalanges appears to have been normal, the fifth metatarsal does not have the long proximal process, and there is no evidence of the peculiar type of navicular which must have been present in *Eutypomys*. The calcaneum of *Palaeocastor* is already that of a typical beaver, whereas that of *Eutypomys* is much longer and more slender, with no indications of the beaver peculiarities.

The *astragalus* and tibia are 15 percent larger than in *Ischyromys*, in which genus they are remarkably small, though the skulls are about the same length. The general proportions of the astragalus are very similar to those of *Paramys robustus*, Amer. Mus. No. 13,091. The dorsal surfaces of the bones in the two forms seem almost identical. On the ventral surface, the ectal facets are very similar. The ental facets, however, differ considerably, being short and broad in *Paramys* and long and narrow, reaching almost to the head, in *Eutypomys*. On the dorsal surface, the head is indistinctly divided into distal and medial facets by a slight groove. In *Paramys*, there is a similar groove on the ventral side of the head, so that in distal view, the head is somewhat flattened, whereas in *Eutypomys*, there is no trace of such a groove, the head being more spheroidal.

The *calcaneum* of *Eutypomys* is quite different from that of *Paramys*. The proximal tuberosity is much less developed. The ectal facet is much more antero-posterior than in *Eutypomys*, where it makes an angle of about 30° with the transverse. The distal facet is more proximad in *Paramys*.

The *cuboid* of *Eutypomys* seems, in dorsal view, much like that of *Paramys*. The *ectocuneiform* is much shorter in *Eutypomys*, being broader than it is long.

Eutypomys has had considerable trouble in finding a suitable taxonomic niche for itself. Matthew (1905) considered that it represented a specialized collateral relative of the beavers. Most authors since that time have followed his lead. Stirton (1935) in his revision of the beavers, observing that *Eutypomys* could not belong with that group, omitted it entirely except for putting it in his evolutionary chart as a possible relative of the stem-beavers, and more nearly related to the Mylagaulidae. Stock (1935) has recently given pretty good evidence that the latter are more closely related to the Allomyidae, which are quite distinct from *Eutypomys*. The development of numerous lakes in the mylagaulids followed quite a different line from that adopted by *Eutypomys*. Miller and Gidley (1918) erected a new family for *Eutypomys*, placing it between the Adjidaumidae and the beavers. While agreeing fully with these authors in the necessity of considering this form a distinct family, I nevertheless feel that it is widely separated from the eomyids, and that it shows no resemblances to early beavers other than the retention of primitive "Sciuromorph" characters, such as the type of infra-orbital foramen and the absence of postorbital processes, or the development of characters that are obviously parallelisms of little significance, such as the emphasis on the outer part of the foot, a character only of the later beavers. *Eutypomys*, however, resembles some of the later beavers (as *Amblycastor*) in the construction of the teeth, a parallelism which may indicate distant relationship. As there is no suggestion of relationship with the geomyoids or Sciuridae, it seems best to consider that the Eutypomyidae are a specialized side branch of the early "Sciuromorphs," which are closest to the Castoridae, and hence have been very tentatively included among the Castoroidea.

If the relationships of this form are much in doubt, its habitus is even more so. In an attempt to discover some form which has a pes similar to that of *Eutypomys*, in order to get a clue as to its function, I have compared it with the feet of *Sciurus*, *Glaucomys*, *Cynomys*, *Marmota*, *Dipodomys*, *Geomys*, *Palaeocastor*, *Castor*, *Erethizon*, *Hystrix*, *Aplodontia*, *Paramys*, *Neotoma* and *Rattus* among the Rodents, and *Galeopithecus*, *Lutra*, *Mustela*, *Phoca*, *Phalanger* and *Mylodon* among other mammals. Nowhere in this assemblage have I found an animal with a foot which at all resembles that of *Eutypomys* in its structural adaptations. As this group includes burrowers, walkers, diggers, climbers, soarers, runners, jumpers and swimmers, and I have been unable to think of any other mode of progression which *Eutypomys* might have used, I am completely mystified as to its habits.

Eutypomys thomsoni Matthew

(Pls. XXIX and XXX, and Pl. XXXI, Figs. 1–2)

(Figs. 40–42 and Matthew, 1905, Figs. 1–3)

Holotype: Amer. Mus. No. 12,254, skull, jaws, both humeri, parts of scapula and tibia, eight vertebrae and parts of eight ribs.

The generic discussion is based on this species, the only one represented by good material. At present, it can be separated from the other species only by its size, the cheek-tooth series measuring 13 to 15 mm. in length.

Other specimens referable to this species are: Amer. Mus. No. 12,255, maxillae with upper molariform teeth, fragments of the skull, axis and tibia, and a fairly complete pes; Amer. Mus. No. 1423, a damaged skull and lower jaw fragments with a partial brain cast; Amherst College No. 20–187, anterior part of skull with lower jaws; Mus. Comp. Zool. Nos. 6190 and 6191, two lower jaws; and Princeton Univ. No. 13,779, a lower jaw.

MEASUREMENTS, *Eutypomys thomsoni*

	Holotype, Amer. Mus. No. 12,254	*Amherst No. 20-187*	*Mus. Comp. Zool. No. 6190*	*Mus. Comp. Zool. No. 6191*	*Princeton Univ. No. 13,779*
	mm.	mm.		mm.	mm.
	left				
P$\underline{3}$–M$\underline{3}$	14.90				
P$\underline{3}$, a-p	1.38	1.78			
transverse	1.61	1.70			
P$\underline{4}$, a-p	3.80	3.57			
width protoloph	3.80	4.00			
width metaloph	3.68	4.00			
M$\underline{1}$, a-p	3.32	3.22			
width protoloph	4.12	4.10			
width metaloph	3.97	4.05			
M$\underline{2}$, a-p	3.18	3.22			
width protoloph	4.23	3.98			
width metaloph	3.83	3.82			
M$\underline{3}$, a-p	2.92	3.78			
width protoloph	3.68	3.53			
width metaloph	2.85	3.02			
	right				
P$\overline{4}$–M$\overline{3}$	14.40			13.50	
P$\overline{4}$, a-p	3.43	3.24	3.06	3.40	3.00
width metalophid	2.57	2.60	2.27	2.78	2.35
width hypolophid	3.14	3.18	3.17	3.40	3.21
M$\overline{1}$, a-p	3.29	3.07	3.07	3.12	3.26
width metalophid	3.32	3.08	3.14	3.33	3.38
width hypolophid	3.31	3.50	3.37	3.49	3.42
M$\overline{2}$, a-p	3.52	3.13	—	3.24	
width metalophid	3.68	3.40	—	3.62	
width hypolophid	3.50	3.50	—	3.75	
M$\overline{3}$, a-p	4.21	4.10	3.78	3.63	
width metalophid	3.26	3.10	3.45	3.46	
width hypolophid	3.02	2.95	3.28	3.22	

Horizon and *Range:* Oreodon Beds (particularly Lower Oreodon Beds) of South Dakota. The Amherst specimen, from Nebraska, is the only one from outside of South Dakota.

Eutypomys parvus Lambe

(Fig. 43, and Lambe, 1908, Pl. 6, Figs. 1–2)

Holotype: Canadian National Museum No. 6482, R P$\overline{4}$.

This form is similar in pattern to *E. thomsoni*, but a third smaller. Even though this species is represented by a single tooth only (which is a right lower premolar, instead of a left third lower molar as Lambe considered it, as may be seen by comparison with the figures of *E. thomsoni*), there can be no doubt of its affinities, nor of the fact that it repre-

sents a species which, at the present time, can be separated from *E. thomsoni* only on the basis of its size. The size distribution of the known specimens strongly suggests that this is a valid method of separating species of this genus.

The measurements of this tooth are: antero-posterior, 2.48 mm.; width metalophid, 1.82; width hypolophid, 2.55 mm.

Horizon: Lower Oligocene of the Cypress Hills.

Eutypomys magnus sp. nov.

(Fig. 45)

Holotype: Princeton Univ. No. 13,779, lower jaw with $P\bar{4}$–$M\bar{3}$ left.

This species differs from *E. thomsoni* in a number of respects. The most obvious is its distinctly larger size. The teeth are simpler, there not being anywhere near as many minor accessory commissures. The crest from the entoconid to the hypoconid is not continuous as in the genotype, but terminates in the basin. The posterior arm of the protoconid and the mesolophid are both long and complete, reaching the lingual margin of the tooth. The connection of the posterior arm of the protoconid with the metaconid appears on the wear surface much later in life than in *E. thomsoni*. The mesolophid shows its real nature much more clearly than in *E. thomsoni*, being definitely separated from the posterior arm of the protoconid. It unites with the entoconid, which is far forward, the posterior side of the tooth being markedly convex instead of nearly straight as in Matthew's species. The margin of $M\bar{2}$ by the rear side of the entoconid is sharply pinched in, the posterolophid not reaching the entoconid. The teeth of the holotype are so widely spaced that the overall measurement is meaningless.

MEASUREMENTS OF *Eutypomys magnus* (Princeton Univ. No. 13,779)

	$P\bar{4}$	$M\bar{1}$	$M\bar{2}$	$M\bar{3}$
antero-posterior	4.02 mm.	4.01 mm.	3.96 mm.	3.82 mm. (wear surface) 4.48 (alveolar)
width, metalophid	3.35	4.04	4.18	3.84
width, hypolophid	4.15	4.42	4.73	3.75

Horizon and *Locality:* Lower Concretionary level, White River of South Dakota.

Eutypomys sp.

(Fig. 44)

A fragment of a lower jaw, with L $P\bar{4}$, in the collection of Mr. C. A. Kinsey of Belgrade, Montana, seems to represent a distinct form of this genus. It is of the same size as *E. thomsoni*, but is not quite as far advanced in the complications of the pattern. It does, however, show an advance over the other species of the genus in the close agreement in height of various cusps and crests of the tooth, the primary cusps not standing out as they do in the other species.

The measurements of this specimen are: a-p, 3.23 mm.; width metalophid, 2.22 mm.; width hypolophid, 3.13 mm.

Horizon: Lower Oligocene of the Thompson Creek Beds of Montana.

Family Eomyidae Depéret and Douxami, 1902

Adjidaumidae Miller and Gidley, 1918.

Miller and Gidley (1918, p. 434) define this family as follows: "Zygomasseteric structure and infra-orbital canal as in the Sciuridae; cheekteeth $\frac{4}{4}$, slightly hypsodont, the enamel pattern unmodified heptamerous." With this last part of their definition I am in complete disagreement, as the first, third and fifth lophs of the eomyid teeth do not seem to me to represent the original styles and stylids, but secondary, even though early, developments. The central crest, in particular, seems to be an entirely different structure, to which the names mesocone and mesoloph, in the upper teeth, and mesoconid and mesolophid, in the lowers, have been applied (Wood and Wilson, 1936, p. 390). Moreover, there is no trace of conules in the upper teeth of these forms. Therefore, I would define the family more in the following manner: Zygomasseteric structure and infra-orbital canal similar to that in the Sciuridae; cheek teeth $\frac{4}{4}$, brachydont to mesodont; pattern of cheek teeth suggestive of cricetids, with strongly developed mesoloph and mesolophid and well developed anterior and posterior cingula.

Genera: *Protadjidaumo, Adjidaumo, Paradjidaumo, Eomys, Omegodus* and *Rhodanomys.*

Range: Middle Uinta to Upper Oligocene of Utah, Colorado, Nebraska, South Dakota and Wyoming, and Upper Eocene and Oligocene of France.

Of the superfamilial relationships of the eomyids, little can be said. There are no other "Sciuromorph" families that approach them in tooth pattern, the nearest being the Eutypomyidae, which are, of course, quite distant. In many respects, the closest parallels are among the Ischyromyoidea, although the zygomasseteric structure is that of a typical "Sciuromorph," whatever that may prove.

Because of the rather close superficial similarity of the pattern of the cheek teeth to that of the Cricetidae, these rodents have frequently been classed as "Myomorphs" in spite of the "Sciuromorph" zygomasseteric construction. A recent example of this point of view is represented by Zittel and Smith Woodward (1925, English translation, Vol. III, p. 110), who say "The dental arrangement, as in *Cricetodon*, makes it possible for these forms to be considered as primitive murinae." These authors, however, show considerable perspicacity in grouping *Gymnoptychus* together with *Eomys* as members of the Eomyinae. Cope recognized that *Gymnoptychus* was not a "Myomorph," and at the same time clearly pointed out the close parallelism between the groups, saying "The structure of the molars in the fossil genus is exactly like that which I have described as found in *Eumys*, extending even to details. This is curious, as that genus is a Myomorph." (1884, p. 820.) The similarity of the teeth of the two genera, of course, is overemphasized in the above quotation.

Schlosser, I believe, was the first person to point out in print the similarity of the adjidaumids and eomyids, saying (1884, p. 136) "*Gymnoptychus* Cope . . . Vielleicht nahe verwandt mit *Eomys* aus den Phosphoriten." Miller and Gidley separate the eomyids quite widely from the adjidaumids, placing *Eomys*, together with the theridomyids, doubtfully in the Zapodidae, where they certainly do not belong, and making no mention of *Rhodanomys* or *Omegodus*. They thus place these two groups, here united as a single family, in separate superfamilies, even though the European eomyids have a typical "Sci-

uromorph" type of infra-orbital foramen. One reason for this undoubtedly can be found in the lack of good skulls of the European forms, and the extreme confusion as to just what constitutes an eomyid, certain forms from Egypt, Mongolia and elsewhere having been referred to this family with no visible justification. I believe that it is safe to say that up to the present no fossils from outside of North America and Europe can be shown to belong to this family.

The European forms agree with the American ones not only in the skull, but also and equally closely, in the cheek-teeth. The resemblance between the American forms and *Rhodanomys* and *Omegodus* (Figs. 46–53) is particularly striking.

The American portion of the family, "as now known, appears to be divisible into two major groups of species. The first of these groups consists of species with brachydont cheek-teeth which retain the antero-external ridge on the inferior molars and have relatively deep anterior and posterior valleys. This division included *Protadjidaumo* . . . and *Adjidaumo*. . . . A second and more progressive group includes species in which the cheek-teeth have higher crowns than those of the last assemblage, and in which the antero-external ridge is lacking from the inferior molars. In these species the pattern showing at the crown of unworn cheek-teeth is similar to that of *Adjidaumo*, although somewhat simpler, but there is the same arrangement of paired anterior and posterior transverse crests, and a median transverse crest extending across the central basin. The anterior and posterior valleys are shallow and crowded, however, and this pattern gives way at an early stage of wear to the familiar one of three transverse lophs. Apparently there is a tendency toward a more lophodont condition in this group commensurate with the increased height of the crowns of the cheek-teeth, and this lophodont condition is being brought about through the elimination of an earlier pattern similar to that of *Protadjidaumo* and *Adjidaumo*. For this group of species the generic name *Paradjidaumo* is proposed." (Burke, 1934, pp. 397–398.)

The correct nomenclature of the American Oligocene members of this family has been in doubt. There are two known genera, for which three names have been used, *Gymnoptychus* Cope, 1873*c*, *Adjidaumo* Hay, 1899, and *Paradjidaumo* Burke, 1934. In his original description, Cope included the species *G. chrysodon*, *G. nasutus*, *G. trilophus* and *G. minutus* in that order, listing the first as "n.g., n.sp.," which, according to the International Rules of Zoölogical Nomenclature (Opinion 7), automatically makes it the genotype. The next year (Cope, 1874), he relegated *G. chrysodon* to synonymy with *Ischyromys typus*, and listed but two species of *Gymnoptychus*, *G. trilophus* (with *G. nasutus* as a synonym) and *G. minutus*. His revised diagnosis was unquestionably a valid diagnosis of an eomyid genus, but the name "*Gymnoptychus*" is not available for it, being, as just shown, a synonym of *Ischyromys*. His subsequent usage (Cope, 1881*a*, 1881*b*, 1883, 1884), which follows the precedent he established at this time, without selecting any species as the genotype of his revised genus *Gymnoptychus*, has led to considerable confusion.

Hay (1899) argued, for entirely erroneous reasons, that *Gymnoptychus* was a synonym of *Ischyromys*, and that the genus containing the other species of Cope's original genus was without a name. He therefore proposed the genus *Adjidaumo*, with *G. minutus* Cope as the genotype. Since that date, some authors have followed Hay, whereas others have retained Cope's name, a situation not conducive to clear thinking. There is no question, however, that Hay will have to be followed.

Burke (1934) erected the genus *Paradjidaumo* to include certain higher crowned members of the family, generically separable from *Adjidaumo minutus*, making the genotype *Eumys minor* Douglass from Pipestone Springs. He presumably selected Douglass' species rather than one of Cope's because of the confusion with regard to Cope's specific names, outlined below.

As Burke (1934, p. 396, note 2) has pointed out, in 1874, "despite the fact that the species *nasutus* had page priority in the first description, Cope relegated it to the synonymy of *trilophus* without giving any reason for his action. I am convinced that Cope's procedure in this and subsequent descriptions contributed to a confusion of types and beclouded the true relationships of the various species described under *Gymnoptychus* in Pal. Bull. 16. . . ." Cope later (1884) referred *G. trilophus* to *G. minutus* as a synonym, and retained *G. nasutus* as a valid species. Burke has shown (op. cit.) that *G. nasutus* and *G. trilophus* are identical. Cope, as first reviewer of the genus, particularly as it was his own genus, could select whatever species he wanted as valid, since they were both published in the same paper. Therefore, since *Gymnoptychus trilophus* Cope, Cope 1874, has priority over *G. nasutus* Cope, Cope 1884, and *Paradjidaumo nasutus* (Cope), Burke 1934, *nasutus* must be a synonym of *trilophus*.

Adjidaumo Hay

(Figs. 46–47 and 54)

Gymnoptychus Cope, 1873*c* (in part).
Ggymnoptychus Cope, Zittel, 1893 (in part).
Gymnoptichus Cope, Trouessart, 1898 (in part).
Adjidaumo Hay, 1899 (in part).
Adjidaumo Hay, Burke, 1934.

Genotype: *Gymnoptychus minutus* Cope, 1873*c*.

The cheek-teeth are brachydont and the cusps rather independent. The anterior and posterior valleys are approximately as deep as the central valley. The anterior cingulum is connected with the middle of the metalophid, rather than with the protoconid as in *Paradjidaumo*. The talonid and trigonid of $M\bar{1}$ have the same width.

Range: Lower Oligocene of Montana; Middle Oligocene of Colorado and South Dakota.

The lower teeth are brachydont and primitive. The four main cusps stand out clearly, especially in the Pipestone species. As is so frequently the case, only the posterior half of $P\bar{4}$ is molariform (Figs. 46–47). The anterior moiety of the tooth is formed of two rounded cusps, connected by their posterior margins to form a high crest. The mesoconid is small, but there is a strong mesolophid running slightly anterad as well as mesiad. In *Paradjidaumo*, the crest runs straight across the tooth. There is a very small posterior cingulum, closely united to the entoconid, and arising from about the middle of the hypolophulid. There does not seem to have been a hypoconulid. This tooth could easily be derived from that of *Protadjidaumo* by slight modifications, especially of the posterior cingulum. The anterior cingulum of the molars extends the whole width of the tooth. It united with the lingual margin of the protoconid, leaving both a lingual and a buccal division of the cingulum, free at both ends. "In *Adjidaumo minimus* (Matthew) the posterior valleys of $M\bar{1}$ and $M\bar{2}$ are relatively narrow and the posterior cingulum crests are weak, while the opposite condition holds in *Adjidaumo douglassi*." (Burke, 1934, p. 395.) *A. minutus* is inter-

mediate in this character. The mesoconid is essentially non-existent in the molars. The mesolophid is short, never reaching the lingual side of the tooth, except in $M\bar{3}$, where it may fuse with the entoconid.

46

47

48

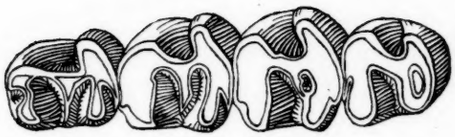

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FIG. 46. *Adjidaumo minutus* (Cope). Holotype. Amer. Mus. No. 5362, $P\bar{4}$–$M\bar{3}$ left.
FIG. 47. *A. minimus* (Matthew). Holotype. Amer. Mus. No. 9625, $P\bar{4}$–$M\bar{3}$ left.
FIG. 48. *Paradjidaumo minor* (Douglass). Amer. Mus. No. 9632, $dP\bar{4}$ left.
FIG. 49. *P. minor* (Douglass). Amer. Mus. No. 9730, $P\bar{4}$–$M\bar{3}$ left.
FIG. 50. *P. trilophus* (Cope). A.E.W. No. 31-8-20-4b, $M\underline{1}$–$dP\underline{4}$ right. (Anterior end of this specimen is to the right.)
FIG. 51. *P. trilophus* (Cope). Amer. Mus. No. 5401, $dP\bar{4}$ left.
FIG. 52. *Omegodus echimyoides* Pomel. Brit. Mus. No. M1629, $P\bar{4}$–$M\bar{3}$ right.
FIG. 53. *Rhodanomys* sp. Basle Bst No. 381, $P\bar{4}$–$M\bar{3}$ right.
All figs. × 10.

D $P\bar{4}$ is quite small, and not quite molariform. The antero-external cusp is much farther forward than the antero-internal, which is as isolated as the paracone of $P\underline{4}$. There is no anterior cingulum, the tooth thus agreeing with $P\bar{4}$.

FIG. 54. *Adjidaumo douglassi* Burke. Holotype. Carn. Mus. No. 1957, $M\bar{1}$–$\bar{3}$ right. After Burke, 1934, Fig. 3. × 10.

The upper molars are essentially mirror images of the lowers, differing chiefly in having somewhat more progressive cingula, which tend to approach the pattern of *Paradjidaumo*, in that the cingula tend to unite with protocone and hypocone, rather than with the protoloph and metaloph. $M\underline{3}$, as is so often the case, is reduced, the trigon resembling that of

the other molars, the talon being almost aborted. The protocone is connected via the mesoloph with the metacone. The hypocone is non-existent, its place being taken by the posterior cingulum, giving a result very similar to that in *Heliscomys* (see above, p. 211). The basin between the paracone and metacone is filled by a large cusp, connected with both the others and with the mesoloph.

P$\underline{4}$ is likewise different from the molars, though it approaches nearer the molariform pattern than does M$\underline{3}$. The paracone is a large, conical cusp, isolated from the protocone. In addition to its isolation, it differs from the corresponding cusp of the molars in being completely conical. The anterior cingulum is short, reaching only the length of the protocone. The anterior half of the tooth is distinctly narrower than the posterior, whereas in the molars the two halves are subequal.

The infra-orbital foramen is far forward on the face, as in the geomyoids. There is, however, a distinct knob at the ventral end of the foramen, not seen in the latter group. The nasals are long and slender, the upper incisors smooth.

The *jaw* is long and slender, the masseteric fossa extending forward to the rear of P$\overline{4}$. This fossa is of unusual shape, the anterior part being very narrow vertically. The ascending ramus slopes back very gently. The coronoid process, which is low and almost non-existent, is distinctly everted. It is much lower than the condyloid. There is a large knob for the base of the incisor, which is separated from the rest of the ascending ramus by a deep groove, as in *Eutypomys* and the Geomyidae. The knob reaches almost to the condyle. The presence of this knob does not indicate relationship, but merely the excessive growth of the lower incisor in all the forms. The mental foramen is high on the mandible, being, in *A. minimus*, almost on the top of the diastema. The mandibular foramen is very far up on the jaw, being well behind the cheek teeth, and as high as the level of the coronoid. The anterior end of the masseteric fossa is turned slightly upward.

An *ischium* (Amer. Mus. No. 5399) referred by Cope to *G. minutus* (1884, Pl. 55, Fig. 27) apparently belongs, on the basis of its size, either to this species or to *Heliscomys*. It is much too small to be associated with the other limb bones Cope referred to *G. minutus*, which are referred below to *Paradjidaumo trilophus*. The ischium is slender, with a fair-sized obturator foramen, and a well marked dorsal process, which, as Cope pointed out (1884, p. 821), does not occur in American cricetids, but does in heteromyids and sciurids. The bone, however, seems slightly too large to have belonged to *Heliscomys*.

The ancestry of *Adjidaumo* is still not clear. The only American form earlier than the White River, definitely referable to the family, is *Protadjidaumo typus* from the Duchesne River. "If not directly ancestral to the genus *Adjidaumo* in later Oligocene horizons, *Protadjidaumo* is certainly closely related to the latter genus. By converting the posterior cingulum of P$\overline{4}$ into a cingulum crest (a process which appears to be under way already), developing a dam near the external exit of the anterior valley of M$\overline{1}$, raising and strengthening its connecting crests and attaining a more crescentic condition of its outer cusps, *Protadjidaumo typus* might easily give rise to such a conservative species of *Adjidaumo* as *Adjidaumo minutus* (Cope). On the other hand, *Protadjidaumo* seems to have progressed too far in the direction of *Adjidaumo* to have led up to the species included in the proposed new genus *Paradjidaumo*." (Burke, 1934, p. 394.)

There has been a very general tendency among authors, at least since 1895 (Scott,

1895) to place this genus with the geomyoids. Matthew (1903) and Winge (1924) may be cited as prominent examples of this tendency. I have been able to find no author who stated the reasons which led him to adopt this arrangement. I believe, however, that originally this arrangement was on the basis of the similarity of the infra-orbital foramen to that of the geomyoids. As has been shown above, while there is considerable similarity in this structure in the two groups, it is not identical. Even if it were, however, I should not believe that their close relationship was demonstrated, or even made probable, in view of the extreme difference in the type of tooth pattern possessed by the two groups. If it shall ever be shown that the geomyoid tooth pattern has been derived by simplification from a pattern such as that of *Sciuravus*, possessing mesocone and mesoconid, and with strong mure and ectolophid, the argument for the distant relationships of the eomyids and geomyoids will be strengthened. For the present, however, as the geomyoid tooth pattern is one of the most isolated of any found in the whole order, it would not be warranted to place the eomyids in a position close to them. The undoubted similarities between certain of the limb bones of eomyids and geomyoids can probably be laid to the fact that both are relatively primitive, ground-dwelling, scampering "Sciuromorphs." Such a habitus has not been proven absolutely for the eomyids, but seems quite probable, from what is known of the skeleton, and from the extreme abundance of these forms in the White River fauna, apparently being among the most abundant of White River rodents, as contrasted with such rarer and perhaps arboreal forms as *Prosciurus*. In this connection it might be mentioned that *Heliscomys* is a much more common form in the White River deposits than one would assume from its rarity in the collections.

A further stimulus to the postulate of geomyoid relationships for the eomyids was given by the publication of Matthew's erroneous figure of *Adjidaumo minimus* (Matthew, 1903, Fig. 11), from which all traces of the mesolophid and the posterior cingulum were omitted, giving the teeth a pattern strikingly suggestive of that of geomyoids. Further prominence was given to this figure by its reproduction by Osborn (1907, Fig. 106).

The correct taxonomic position of these animals was re-emphasized by Miller and Gidley (1918), who made them a distinct family (the Adjidaumidae) among the Sciuroidae. They were followed by Hay (1930). Wood (1931) specifically pointed out that there could be no relationship between the adjidaumids and the heteromyids though not ruling out relationships with geomyids. Such relationship is, of course, impossible. Other authors have tacitly accepted the same point of view. I believe that the present occasion is the first when the adjidaumids and eomyids have been united as a single and distinct family among the "Sciuromorphs."

Adjidaumo minutus (Cope)

(Fig. 46, and Cope, 1884, Pl. LXV, Figs. 19–20, 22–30)

Gymnoptychus minutus, Cope, 1873*c*.

Holotype: Amer. Mus. No. 5362, lower jaw with $P\bar{4}$–$M\bar{3}$ left.

The cheek-teeth are about 4.5 mm. long, being the largest known species of the genus. The mesolophid tends to unite with the entoconid on the last two lower molars. The measurements of the skull are given in considerable detail by Cope (1884, pp. 824–825).

MEASUREMENTS OF CHEEK TEETH OF *Adjidaumo minutus*

	Holotype, Amer. Mus. No. 5362		*Holotype, Amer. Mus. No. 5362*
$P\overline{4}$–$M\overline{3}$	4.70 mm.	$M\overline{2}$ a-p	1.25 mm.
$P\overline{4}$ a-p	1.05	width metalophid	1.28
width anterior loph	0.85	width hypolophid	1.19
width posterior loph	0.92	$M\overline{3}$ a-p	1.17
$M\overline{1}$ a-p	1.26	width metalophid	1.05
width metalophid	1.18	width hypolophid	0.97
width hypolophid	1.20		

Range: Middle Oligocene Cedar Creek Beds of Colorado and White River of South Dakota.

Adjidaumo minimus (Matthew)

(Fig. 47; Matthew, 1903, Fig. 11; and Osborn, 1907, Fig. 106)

Gymnoptychus minimus Matthew 1903.

Holotype: Amer. Mus. No. 9625, lower jaw with $P\overline{4}$–$M\overline{3}$ left.

The cheek teeth are about 3.5 mm. long. The mesolophid is free from the entoconid on $M\overline{2}$ and nearly so on $M\overline{3}$.

MEASUREMENTS OF *Adjidaumo minimus*

	Holotype, Amer. Mus. No. 9625		*Holotype, Amer. Mus. No. 9625*
$P\overline{4}$–$M\overline{3}$	3.62 mm.	$M\overline{2}$, a-p	0.91 mm.
$P\overline{4}$, antero-posterior	0.92	width, metalophid	0.96
width, anterior loph	0.68	width, hypolophid	0.89
width, posterior loph	0.85	$M\overline{3}$, a-p	0.93
$M\overline{1}$, a-p	1.00	width, metalophid	0.90
width, metalophid	0.92	width, hypolophid	0.76
width, hypolophid	0.88		

Horizon and *Locality:* Lower Oligocene of Pipestone Springs, Montana.

Adjidaumo douglassi Burke

Burke, 1934

(Fig. 54, and Burke, 1934, Fig. 3)

Holotype: Carn. Mus. No. 1957, lower jaw with $M\overline{1}$–$\overline{3}$, right.

"A little larger than *Adjidaumo minimus* (Matthew) and smaller than *Adjidaumo minutus* (Cope); inferior molars with crescentic external cusps, steep outer walls, crowded anterior valleys, deep central basins, and reduced anterior cingula; posterior valley wide on $M\overline{1}$ and $M\overline{2}$, merely indicated on $M\overline{3}$, median transverse crest of $M\overline{3}$ joined with entoconid, forming fossette internal to hypoconid, crest from entoconid in $M\overline{1}$–$\overline{2}$ oblique and joined with postero-external wall postero-internal to hypoconid." (Burke, 1934, p. 395.)

"In size this species approaches *Adjidaumo minimus* (Matthew) but shows considerable advance over the latter and a somewhat lesser advance over *Adjidaumo minutus* (Cope) in the more crescentic condition of its external cusps, in having higher and more oblique connecting crests, and deeper central basins which are tending to become fossettes. In *Adjidaumo minimus* (Matthew) the posterior valleys of $M\bar{1}$ and $M\bar{2}$ are relatively narrow and the posterior cingulum crests weak, while the opposite conditions hold in *Adjidaumo douglassi*." (Op. cit., p. 395.)

Range: Upper Oligocene of White Butte, North Dakota.

Paradjidaumo Burke

Gymnoptychus Cope, 1873*c* (in part).
Ggymnoptychus Cope, Zittel, 1893 (in part).
Gymnoptichus Cope, Trouessart, 1898 (in part).
Adjidaumo Hay, 1899 (in part).
Paradjidaumo Burke, 1934.
Genotype: *Eumys minor* Douglass 1901.

"$P\frac{1}{1}$, $M\frac{3}{3}$. Cheek-teeth more hypsodont and progressively more lophodont than in *Adjidaumo:* pattern of unworn cheek-teeth resembling that of *Adjidaumo*, but somewhat simpler; anterior and posterior valleys shallow and narrow. Cingula, excepting anterior cingula of $P\frac{4}{4}$ elevated into marginal crests; antero-external ridge lacking from inferior molars; '*Adjidaumo*' pattern evanescent, moderate wear reduced superior surface of crown to characteristic omega-like design of three transverse lophs." (Burke, 1934, p. 397.) The trigonid of $M\bar{1}$ is narrower than the talonid.

As indicated by Burke, this genus is characterized by a mesodont dentition and by the great reduction of the anterior and posterior valleys, so that the cingula soon unite with the metalophid and hypolophid respectively. This is a point of similarity with the European members of the family (see Figs. 52–53). In addition, instead of uniting with the middle of those lophs, as in *Adjidaumo*, they unite with the buccal end of the loph, so that there is no free buccal cingulum. In this respect, *Paradjidaumo* is the most progressive member of the family. As was indicated by Burke, slight wear produces the omega-like pattern, which gave rise to the name "*trilophus*," as well as to the generic name of *Omegodus*. There seems to be a short anterior cingulum on the premolar. There is considerable variation in the length of the mesolophids, which may be as short as in *Adjidaumo*, or may extend to the lingual margin of the teeth. This latter condition seems particularly prevalent in *Paradjidaumo minor*, about half the specimens that I have seen being of this type. One specimen of *P. minor*, Amer. Mus. No. 9634, shows a connection between the anterior cingulum and the middle of the metalophid of $M\bar{3}$. I have seen this in no other member of the genus. It is, of course, the remnant of the pattern characteristic of *Adjidaumo*. The mesolophid unites with the entoconid in $M\bar{3}$ and frequently in $M\bar{2}$. $DP\bar{4}$ is similar to $P\bar{4}$, and is as long but more slender.

The upper teeth are characterized by very long mesolophs, often reaching the buccal margin of the tooth and uniting with the paracone and metacone, forming a marginal crest. $P\underline{4}$ is practically molariform.

The specializations of this genus, as indicated by the figures, are quite different from those of *Rhodanomys*, which seems to be a further development of an *Adjidaumo*-like form, and likewise distinct from *Omegodus*, which has not completed the fusion of the anterior cingulum with the protoconid, and in which the cingulum is emphasized at the expense of the metalophid.

Cope (1884, pp. 823–824) states concerning the lower incisor that "a feature of this tooth, where it differs from the corresponding one of the upper jaw, is seen along the line where the anterior passes into the external surface. Here is a delicate groove, which is bounded on the outer side by an equally delicate thread-like ridge. In some specimens a still more delicate groove extends along at the front of the inner angle." These features characterize all specimens I have seen.

The mandible seems identical with that of *Adjidaumo* except that the masseteric fossa does not extend quite so far forward.

"The maxillo-premaxillary suture is quite sinuous in its inferior portions, and passes in front of the infra-orbital foramen, . . . one-fourth of the distance from the latter to the . . . incisive alveolus . . . The incisive foramina extend chiefly in advance of this suture, notching the maxillary bone a little. A shallow groove extends posteriorly from each incisive foramen along the palate . . . , becoming shallower posteriorly. The tuberosity behind the inferior extremity of the infra-orbital foramen, usual in the Sciuridae, is here represented by a scar, with an inferior angular border. A shallow and wide fossa occupies the entire side of the maxillary bone above the infra-orbital foramen and behind the premaxillary suture. [This fossa indicates that the masseter reached well forward of and above the infra-orbital foramen, being fully as specialized in this respect as in modern "Sciuromorphs."] The side of the premaxillary anterior to the suture is also shallowly concave. The maxillary is also slightly concave in front of the inferior base of the zygomatic arch. The base of the latter has considerable vertical extent, but the arch is not preserved in any . . . specimens. The premaxillary bone is continued upwards and backwards to the frontal, ceasing with [anterior to] the posterior extremity of the nasal. Of the superior maxillary teeth, the first and third are equal, while the second is a little larger. The fourth has about three-fourths the linear dimensions of the third. The outlines of all are, in horizontal section, quadrate with rounded angles. The incisors are much compressed, and the anterior face of each is strongly and equally convex [they really seem nearly flat]. The inner angle is pronounced, while the external is rounded." (Cope, 1884, pp. 822–823.)

"The *humerus* is rather slender, and the deltoid crest does not exhibit the prominence so usual in the *Muridae*. It is most prominent on the antero-external aspect of the shaft near its middle; an external as well as an anterior ridge diverges from it upwards. The condyles have no intertrochlear ridge, and the external trochlea is not more extended transversely than the internal, measuring from the fundus of the groove. There is a moderate internal epicondyle, and the arterial foramen is distal, and opens anteriorly below and on the external face above." (Cope, 1884, p. 821.) The supinator crest is well marked. The distal end, however, is quite narrow, approaching that of typical running rodents, rather than scamperers or climbers. The bone is "Sciuromorph" rather than "Myomorph" in its heritage characters, but its habitus characters suggest an aberrant adaptation.

The proximal end of a *femur*, referred by Cope to *G. minutus*, probably belongs to

this genus. It differs from the corresponding bone of cricetids, and agrees with that of sciurids, in the sharp and angulate nature of the lesser trochanter, and the lack of overhang of the trochanteric fossa by the great trochanter. It is perhaps too small to belong to *Eumys*, as suggested by Cope, but the size difference is slight. It might belong to *Prosciurus*, but seems most probably either *E. elegans* or *P. trilophus*. "The great trochanter is elevated as high as the head, from which a deep notch separates it; its posterior fossa is pronounced. The little trochanter is very prominent, projecting at right angles to the shaft. The shaft is broken, so that the presence of a third trochanter cannot be ascertained. The distal end of the femur is characterized by a patellar groove of moderate width, with fairly elevated ridges which are continued well posteriorly on the shaft, but not further than in existing *Sciuridae*, and not as far as in *Palaeolagus*." (Cope, 1884, pp. 821–822.) Cope then proceeds to describe a distal end of a tibia and a calcaneum, neither of which I have been able to find in the American Museum collections.

The original collections of *Paradjidaumo* were from the Cedar Creek Beds of Colorado. Most of the other known specimens come from Pipestone Springs. The genus is, however, quite abundantly represented in the Oreodon Beds of the Big Badlands, though many of the specimens are single teeth. There appear to be two forms present, one of which is distinctly larger than *P. trilophus*, and the other about the same size as Cope's species, but showing a greater reduction of the posterior cingulum.

Paradjidaumo minor (Douglass)

Eumys minor Douglass 1901.
Gymnoptychus minor (Douglass), Matthew 1903.
Adjidaumo minor (Douglass), Hay 1930.
Paradjidaumo minor (Douglass), Burke 1934.

(Figs. 48, 49, 55 and Burke, 1934, Fig. 4)

Holotype: Carn. Mus. No. 735, lower jaw with $P\bar{4}$–$M\bar{1}$ right.

The mesolophid is long, and in $M\bar{2}$ unites with the entoconid. The anterior cingulum is not fully joined to the protoconid in unworn teeth. The buccal cusps of the molars are slender. The anterior cusps of $P\bar{4}$ are distinctly separated. The lower milk premolar is quite different from the permanent teeth, the antero-lingual cusp being connected by a lingual crest with the end of the mesolophid, while the ectolophid is incomplete.

In the American Museum material from Pipestone Springs, there seem to be two distinct size groups, the larger of which agrees in size with the holotype (on the basis of measurements made from Burke's figure and checked with Douglass' measurements), though the larger specimens have a greater antero-posterior diameter of $M\bar{1}$ than in the holotype.

FIG. 55. *Paradjidaumo minor* (Douglass). Holotype. Carn. Mus. No. 735, $P\bar{4}$–$M\bar{1}$ right. After Burke, 1934, Fig. 4. × 10.

MEASUREMENTS OF *Paradjidaumo minor*

	Amer. Mus. No. 9627	*Amer. Mus. No. 9628*	*Amer. Mus. No. 9629*	*Amer. Mus. No. 9635*	*Amer. Mus. No. 9631*	*Amer. Mus. No. 9632*	*Amer. Mus. No. 9633*	*Amer. Mus. No. 9634*	*Amer. Mus. No. 9630*
	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
$P\bar{4}$–$M\bar{3}$	5.36	—	—	5.38	—	—	—	5.80	6.05
$P\bar{4}$ a-p	1.34	1.55	—	1.26	1.39	d1.19	1.55	1.62	1.58
width anterior loph	1.03	1.25	—	1.10	1.05	d0.79	1.09	1.20	1.26
width posterior loph	1.31	1.50	—	1.27	1.14	d0.91	1.31	1.34	1.37
$M\bar{1}$ a-p	1.44	1.71	1.32	1.44	1.47	1.38	1.52	1.47	1.62
width metalophid	1.28	1.50	1.38	1.34	1.33	1.27	1.37	1.32	1.54
width hypolophid	1.33	1.52	1.40	1.48	1.31	1.33	1.40	1.43	1.65
$M\bar{2}$ a-p	1.44	1.49	1.40	1.31	1.47	1.57	1.48	1.38	1.57
width metalophid	1.38	—	—	1.44	1.33	1.32	1.37	1.42	1.62
width hypolophid	1.43	—	1.40	1.47	1.19	1.35	1.38	1.41	1.70
$M\bar{3}$ a-p	1.42	—	—	1.41	—	—	—	1.50	1.50
width metalophid	1.25	—	—	1.19	—	—	—	1.29	1.48
width hypolophid	1.25	—	—	1.10	—	—	—	1.18	1.30

d = deciduous tooth.

Range: Titanotherium Beds, Pipestone Springs, Montana.

Paradjidaumo trilophus (Cope)

Gymnoptychus nasutus, Cope 1873*c* (in part).
Gymnoptychus trilophus, Cope 1873*c*.
Gymnoptychus trilophus Cope, Cope 1874 (in part).
Adjidaumo trilophus (Cope), Hay 1899.
Adjidaumo nasutus (Cope), Hay 1899.
Gymnoptychus liolophus, Matthew 1903 (*Nomen nudum*).
Paradjidaumo nasutus (Cope), Burke 1934.

(Figs. 50, 51 and 56; Burke, 1934, Fig. 5; Cope, 1883, Fig. 5*e*; 1884, Pl. LXV, Figs. 21, 21–34)
Holotype: Amer. Mus. No. 5401, lower jaw with $dP\bar{4}$–$M\bar{2}$ right.

The mesolophid is short, and is free lingually on all the teeth. The anterior cingulum is fully joined to the protoconid in unworn teeth. In size this form is slightly larger than is *P. minor*. The anterior cusps of the lower premolar are close together. The lower milk tooth is essentially molariform.

FIG. 56. *Paradjidaumo trilophus* (Cope). Carn. Mus. No. 1033, $P\bar{4}$–$M\bar{3}$ left. After Burke, 1934, Fig. 5. × 10.

I have included in the measurements of this species some of the material from the Big Badlands that seems to come the closest to the type represented by the Cedar Creek speci-

mens. I have not had an opportunity to go sufficiently deeply into the subject to be certain whether or not they are conspecific with the Colorado material.

MEASUREMENTS OF *Paradjidaumo trilophus*

	Amer. Mus. No. 5401	*Carn. Mus. No. 1033*	*A.E.W. No. 31–8–20–4a*	*A.E.W. No. 31–8–20–4b*
	mm.	mm.	mm.	mm.
$P\bar{4}$–$M\bar{3}$	—	5.62	—	
$P\bar{4}$ a-p	d1.50	1.52	1.62	
width anterior loph	d0.85	1.16	1.33	
width posterior loph	d1.14	1.27	1.47	
$M\bar{1}$ a-p	1.57	1.37	1.53	
width metalophid	1.53	1.22	1.68	
width hypolophid	1.60	1.37	1.63	
$M\bar{2}$ a-p	1.57	1.22	—	
width metalophid	1.65	1.27	—	
width hypolophid	1.64	1.32	—	
$M\bar{3}$ a-p	—	1.38	—	
width metalophid	—	1.20	—	
width hypolophid	—	1.10	—	
$dP\underline{4}$ a-p				1.29
width protoloph				1.23
width metaloph				1.25
$M\underline{1}$, a-p				1.57
width protoloph				1.60
width metaloph				1.63

d = deciduous teeth. Carn. Mus. No. 1033 after Burke's figure.

Range: Middle Oligocene Cedar Creek of Colorado and Oreodon Beds of Wyoming, Nebraska and South Dakota.

Suborder "**MYOMORPHA**" Brandt 1851

Rodent families in which the masseter medialis has somewhat enlarged the infra-orbital foramen and pushed forward upon the face in front of the zygoma. The angular process of the mandible arises in the plane of the ramus. Dental formula $P\frac{1-0}{0}$, $M\frac{2-3}{2-3}$.

Range: Middle Oligocene to Recent of the entire world.

A number of the families that are grouped in this suborder are rather definitely and closely related. Others that could fit nowhere else in any classification that has been suggested as yet, fit here with extreme difficulty. Fortunately, the only members of the suborder that occur in the White River are cricetids, which unquestionably belong here on our present concepts.

Superfamily **MYOIDEA** Gill 1872

This group includes the Muridae and such families as are most closely related to it. At the present time it is quite uncertain what families, if any, are close to the murids.

They appear to be as completely isolated from the rest of the order as are the geomyoids. It is probable that a new superfamily should be erected to include the cricetids and their relatives. For the present, however, it has been thought best to be conservative and to leave the cricetids with the murids.

Family CRICETIDAE Rochebrune 1883

This family may be briefly defined as murine "Myomorphs" with a tooth pattern based on four primary cusps, a mesocone or a mesoconid, together with a series of diagonal connecting crests. The infra-orbital foramen is very narrow, expanding dorsally into a rounded fenestra for the masseter. The cheek teeth seem always to be $M\frac{3}{3}$.

Eumys Leidy

(Pl. XXXI, Figs. 3 and 3*a* and Pls. XXXII and XXXIII)

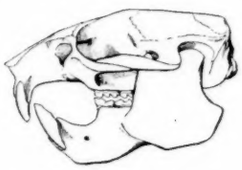

FIG. E. Skull and jaws of *Eumys*. Approximately natural size.

Eumys Leidy, 1856.

Eumys (Leidy nom.) Cope, Cope 1884.

Genotype: *E. elegans* Leidy, 1856.

This is a brachydont cricetid with the tooth pattern still clearly based on the four primary cusps plus the mesocone (or mesoconid) and the connecting crests. The posterior arm of the protoconid is always longer than the mesolophid, in contradistinction to *Cricetodon*, where the two crests are of the same length or the mesolophid is longer. The infra-orbital foramen is narrowed in the typical cricetid manner. The temporal crests unite above the eyes to form a sagittal crest. The snout is heavy.

Range: Middle and Upper Oligocene of the United States, ?Upper Oligocene of Mongolia.

The upper teeth of *Eumys* are rather characteristic. M1 shows the strong anterocone of the cricetids, connected by a well marked crest with the protocone (Figs. 57 and 59). The paracone, while united with the protocone, is more clearly connected, via the mure and mesocone, with the hypocone. There is a similar diagonal impression visible in the other molars. This diagonal trend seems to be much more strongly marked than in *Cricetodon* (Schaub, 1925, Pls. 1–2), and represents the fundamental ground plan for the upper cheek teeth of all the New World cricetids. In M3, the hypocone is very small or aborted, a further distinction from the European members of the family. The European genera have tended toward a transverse rather than a diagonal alignment of the cusps.

In the lower jaw, the most striking characteristic of the molars of *Eumys* is the short mesolophid and the long posterior arm of the protoconid, the latter always being longer than the former. There are numerous variations in detail of these teeth, some of which are taken up more minutely in the discussion of the various species. A consideration

of the others will be reserved for a future study, which I hope to be able to make, dealing only with these interesting forms.

The overall dimensions of the skull of *Eumys* are about the same as those of *Peromyscus californicus*, the largest of the recent *Peromyscus*. There are, however, considerable differences in proportion. The rostrum is very much heavier in *Eumys*, being distinctly wider than the postorbital constriction, whereas in *Peromyscus* the opposite is true. The rostrum is perhaps slightly heavier, proportionately, in *Eumys* than in any *Cricetodon* I have seen figured. Cope (1884, p. 851) remarked on this feature of *Eumys*, saying "With molar teeth as large as those of the Norway rat the muzzle of the *Eumys elegans* is not more than two-thirds as long, so that the species was in general proportions smaller and more robust. . . . The hundred and more individuals represented by my specimens evidently differed in minor respects, as in size and robustness. Some, perhaps males, have the muzzle stouter in proportion to the length than others; some are more decurved than others."

The anterior ends of the nasals are somewhat flaring and tubular as in *Peromyscus*, and definitely more so than seems to have been the case with *Cricetodon*. Posteriorly, the nasals narrow and, together with the premaxillaries, are received into a notch in the front of the frontals. There are faint superciliary ridges in both *Eumys* and *Peromyscus*. In the latter, these diverge rapidly behind the orbit. In *Eumys*, on the contrary, the crests meet at the narrow point of the skull, and are continued from there on back as a sagittal crest. This difference is largely dependent on the size of the brain, that of *Eumys* being quite small whereas that of *Peromyscus* is large and considerably expanded. This sort of a change would be normally expected between an Oligocene and a Recent form. The interparietal is large, with a rounded anterior end. It is bounded anteriorly and laterally by the parietals, which reach to the occipital. Posteriorly the interparietal is concave, the occiput swinging well forward.

The zygomata flare distinctly more in *Eumys*, the zygomatic breadth being greater in this form than in *Peromyscus*. The arch is quite heavy, showing no signs of the reduction characteristic of the recent genus. It seems thicker even than in *Cricetodon*, being visibly heavier than in *C. incertum* (Schaub, 1925, Fig. 11) from the Oligocene, and distinctly more so than in the Miocene *C. minus* (op. cit., Fig. 4). The lachrymal is reduced practically to the vanishing point in both *Eumys* and *Peromyscus*, being confined exclusively to the orbit in both. The glenoid is further caudad than in *Peromyscus*, the rear part of the skull apparently being longer in proportion to the antorbital section than in the Recent genus.

In lateral view, the skull of *Eumys* is much heavier than that of *Peromyscus*. Instead of a rounded braincase, with the dorsum of the anterior portion of the skull flat, as in *Peromyscus*, the skull is slightly arched, the interorbital region being somewhat higher than the rest. The rostrum is quite deep. The zygoma is nearly horizontal, instead of curving down to the level of the cheek teeth as in *Peromyscus*. The arching of the middle of the skull is by no means as pronounced as is indicated for *Cricetodon* by Schaub's figures. In *Peromyscus*, the malar is extremely reduced in length, whereas in *Eumys* it extends forward to the level of the rear end of the masseteric plate. The glenoid fossa is large and deep, and covered by a wide shelf from the squamosal. The occiput is wide, and the lateral fifth on each side is formed by the swollen, though apparently not inflated, mastoids.

These extend into the glenoid fossa, above the bulla. The bulla is short antero-posteriorly, and elongate in a more transverse direction, with a prominent styloid process at the anterior end. The paroccipital process, very close to the condyle, is relatively small.

The infra-orbital foramen is much more primitive than that of *Perognathus*, and rather different from that of *Cricetodon*, in having a large dorsal section, more nearly circular than in either of the other genera, while the ventral section is distinctly narrower. In this, *Eumys* is further from *Cricetops* than is *Cricetodon*. As in *Cricetodon*, the dorsal extension of the masseteric fossa is much more limited than in *Peromyscus*. The plate in *Eumys* is much broader than in the Recent form, and somewhat more so than in *Cricetodon*. The infra-orbital foramen is much less primitive than in *C. incertum* (Schaub, 1925, Figs. 11–12), where the lower section of the foramen, for the passage of nerve and bloodvessels, is completely uncompressed and the masseteric plate has hardly begun to grow upwards. In some specimens of *Eumys*, this ventral portion is as highly compressed as an opening could be, and still remain an opening.

The palatal view is quite strikingly different from that of both *Cricetodon* and *Peromyscus*. The incisive foramina are some distance from the incisors, and are quite short, instead of beginning just behind the teeth and being elongate, as in the other two genera. Their posterior end is at approximately the same position in all three forms—the anterior end of the tooth row. Although the foramina are of equal length in *Peromyscus* and *Cricetodon*, their shape in *Peromyscus* is much more like that of *Eumys*, as they are broad posteriorly and taper toward the front. The zygomata extend out from the rostrum at an obtuse angle as in *Peromyscus*, instead of a right angle as in *Cricetodon*. The ventral view emphasizes the short rostrum and heavy incisors of *Eumys*, as contrasted with the long rostrum and weak incisors of the other two genera. The heavy zygomata, as has already been indicated, are horizontal and do not tend to be concave in ventral view as in *Peromyscus* and *Cricetodon*. The palate is much longer than in either of the other genera, ending in all three at the rear end of M3. This brings up the most striking difference between *Eumys* and the other genera in palatal view—the large size of the cheek teeth in *Eumys* when contrasted with their small size and apparent reduction in *Peromyscus* and *Cricetodon*. The pterygoid fossae seem similar in all three forms.

In the characters of the skull, then, *Eumys* seems to combine certain features characteristic of recent American cricetids with others that are observed in *Cricetodon*, and seem to represent primitive cricetid characters, plus a few that seem to indicate specializations in a direction of its own. In the structure of the zygomasseteric area, some species of *Cricetodon* are distinctly more primitive than *Eumys*. In the size and general appearance of the teeth, these two Oligocene genera stand as the stem forms of two lines of radiation, one Old World, the other New. It is difficult to determine which has the more primitive teeth, though I should be inclined to consider those of *Eumys* somewhat more so. As long as we do not know from what form the cricetids have been derived, however, such considerations must be nothing but personal opinion.

In view of the great abundance of *Eumys* jaws and skull fragments, it is extremely surprising that there is no skeletal material that can with certainty be referred to this genus.

No pre-Oligocene "Myomorphs" have as yet been found, nor are there any known forms that could be considered as being ancestral to them, unless *Pauromys* Troxell (1923) should turn out to be an ancestor, as suggested by Schaub (1925, p. 109). At first glance,

it would seem that the tooth pattern of the molars of *Pauromys* (Fig. 65) would readily serve as the basis for the pattern of *Eumys* molars. The premolar of *Pauromys* is sufficiently small to warrant the assumption that it was about to be lost. On closer inspection, however, it is clear that the teeth of *Pauromys* possess a hypolophulid II, whereas in *Eumys* the crest that is present is the hypolophulid I. This strongly suggests that *Pauromys* is simply a slightly aberrant sciuravid, and that it is moving in an entirely different direction from the cricetids, there being no instances that I know of in which a form with one type of hypolophulid has been transformed into one with the other. *Simimys* Wilson (1935) seems to have much closer relationships to the sicistids or zapodids than to the cricetids.

It is at present utterly impossible to trace the evolution of the later Tertiary and Recent cricetids of America either from *Eumys* or from anything else. In fact, the only forms that can be definitely derived from *Eumys* at present are *Scottimus* (see below, pp. 255, 257) and *Leidymys*, which in turn do not seem to lead to any other forms. *Paciculus*, of the John Day, is quite distinct from *Eumys*, in the slender paracone and metacone, the emphasis of the transverse arrangement of the crests, and the great enlargement of the mesoloph.

The study of *Eumys* is complicated by the extreme wealth of material available, together with the great range of variation within this material. Whether this variation is individual, sexual, subspecific, specific, geographic or phylogenetic or a combination of several of these, is completely unknown at present.

Eumys elegans Leidy

Leidy, 1856

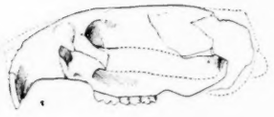

FIG. F. Skull of *Eumys elegans*. Approximately natural size.

(Figs. 57–58, Leidy, 1869, Pl. XXVI, Figs. 12–13; Cope, 1884, Pl. LXV, Figs. 1–14; Wood, 1936*a*, Fig. 1)

Holotype: Acad. Nat. Sci. No. 11,027, left mandible with $M\bar{2}$, part of $M\bar{1}$ and the alveolus of $M\bar{3}$.

$M\bar{2}$ is quadrate, longer than broad, with the anterior cingulum continuous across the whole front of the tooth, the buccal and lingual portions being subequal. The posterior arm of the protoconid of this tooth is free from both the metaconid and the entoconid, reaching almost to the lingual margin of the tooth. The mesoconid is small, with the lingual portion of the mesolophid absent and the buccal portion very weak. The hypoconulid is apparently reduced. The posterior cingulum reaches the entoconid upon wear.

Due to the fragmentary nature of the holotype, it has been rather difficult to determine just which specimens are referable to *E. elegans*. In practise, it has seemed best to class all specimens as members of this species unless the contrary can be established. It is possible to identify lower jaws as being this species, with a fair approximation to accuracy,

on the basis of the structure of $M\bar{2}$ and the overall dimensions of the teeth. Since there are only two specimens that I know of belonging to this genus in which there is an association of upper and lower teeth (the holotypes of *E. parvidens* and *E. exiguus*, described

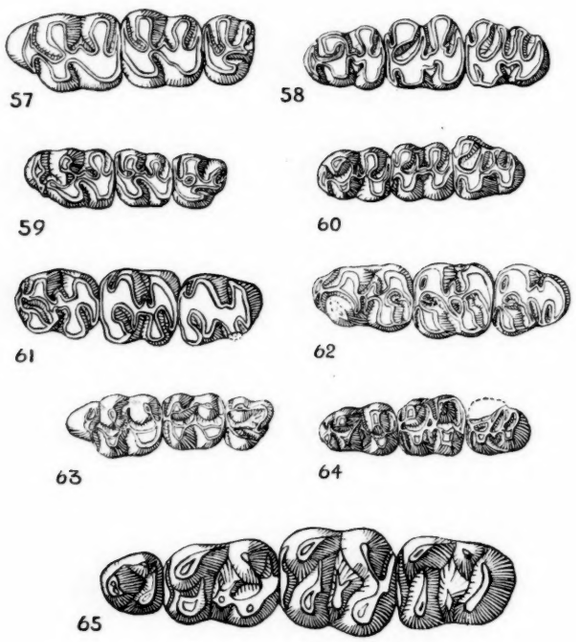

FIG. 57. *Eumys elegans* Leidy. U. Nebr. No. 7-22-8-34-SP, $M\underline{1}$–$\underline{3}$ left.
FIG. 58. *Eumys elegans* Leidy. Brit. Mus. No. M11,631, $M\bar{1}$–$\bar{3}$ left.
FIG. 59. *Eumys parvidens* n. sp. Holotype. U. Nebr. No. 22-1-8-33-SP. $M\underline{1}$–$\underline{3}$ left.
FIG. 60. *Eumys parvidens* n. sp. Holotype. U. Nebr. No. 22-1-8-33-SP. $M\bar{1}$–$\bar{3}$ left.
FIG. 61. *Eumys brachyodus* n. sp. Holotype. M.C.Z. No. 5069, $M\bar{1}$–$\bar{3}$ right.
FIG. 62. *Eumys obliquidens* n. sp. Holotype. Amer. Mus. No. 5603, $M\bar{1}$–$\bar{3}$ right.
FIG. 63. *Eumys exiguus* n. sp. Holotype. Amer. Mus. No. 12,261, $M\underline{1}$–$\underline{3}$ left.
FIG. 64. *Eumys exiguus* n. sp. Holotype. Amer. Mus. No. 12,261, $M\bar{1}$–$\bar{3}$ left.
FIG. 65. *Pauromys perditus* Troxell. Holotype. Y.P.M. No. 13,601, $P\bar{4}$–$M\bar{3}$ left.
Fig. 65 × 15. The others all × 5.

below), the only method of associating upper teeth with *E. elegans* is by their dimensions. The upper teeth figured as of *E. elegans* (Fig. 57) have been identified in this manner, so that the specific identity must be used with caution.

Range: This species occurs in the Oreodon Beds of South Dakota, Montana, Nebraska and Colorado, and the Upper Oligocene of Nebraska.

MEASUREMENTS OF *Eumys elegans*

	Acad. Nat. Sci. No. 11,027	*Amer. Mus. No. 5602*	*Brit. Mus. No. M. 11,631*
	mm.	mm.	mm.
$M\bar{1}$–$\bar{3}$	7.00	6.97	6.92
$M\bar{1}$ a-p	—	2.59	2.29
width metalophid	—	1.41	1.50
width hypolophid	—	1.84	1.75
$M\bar{2}$ a-p	2.26	2.20	2.23
width metalophid	1.96	1.98	1.90
width hypolophid	1.95	1.97	2.09
$M\bar{3}$ a-p	—	2.13	2.42
width metalophid	—	1.86	1.85
width hypolophid	—	1.43	1.48

	Univ. Nebr. No. 7–22–8–34–SP	*Amer. Mus. No. 12,258*
$M\underline{1}$–$\underline{3}$	7.15 mm.	6.80 mm.
$M\underline{1}$ a-p	3.25	3.00
width anteroloph	1.55	1.40
width protoloph	2.23	1.84
width metaloph	2.14	1.99
$M\underline{2}$ a-p	2.25	2.09
width protoloph	2.18	1.96
width metaloph	1.96	1.75
$M\underline{3}$ a-p	1.48	1.68
width protoloph	1.95	1.91
width metaloph	1.48	1.16

Eumys parvidens sp. nov.

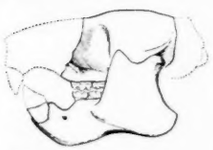

FIG. G. Skull and jaws of *Eumys parvidens*. Approximately natural size.

(Figs. 59–60 and Pl. XXXI, Fig. 3)

Holotype: U. Nebr. No. 22–1–8–33–SP, a partial skull with associated lower jaws.

This is a small species, being about 15 percent smaller than *E. elegans*. $M\frac{3}{3}$ are large. The mesolophs and mesolophids are fairly well developed, but not strikingly so. In general, this form has a primitive *Eumys* pattern on a small scale.

This species is extremely important in that the holotype is the only specimen of *Eumys* with which I am familiar where there is certain association of the skull and jaws, since the jaws were articulated with the skull when I first saw the specimen, and were skillfully separated at my request by Mr. Henry Reider, preparator at the University of Nebraska.

MEASUREMENTS OF *Eumys parvidens*

	Univ. Nebr. No. 22-1-8-33-SP	*Amer. Mus. No. 5535*	*U. S. Nat. Mus. No. 1946*
	mm.	mm.	mm.
M$\overline{1}$–$\overline{3}$	5.90	6.05	—
M$\overline{1}$ a-p	2.08	2.15	2.06
width metalophid	1.32	1.29	1.09
width hypolophid	1.50	1.44	1.39
M$\overline{2}$ a-p	1.78	1.81	1.82
width metalophid	1.62	1.63	1.50
width hypolophid	1.62	1.63	1.55
M$\overline{3}$ a-p	2.01	1.99	—
width metalophid	1.73	1.69	—
width hypolophid	1.13	1.22	—
M$\underline{1}$–$\underline{3}$	5.74		
M$\underline{1}$ a-p	2.56		
width anteroloph	1.20		
width protoloph	1.63		
width metaloph	1.58		
M$\underline{2}$ a-p	1.63		
width protoloph	1.67		
width metaloph	1.52		
M$\underline{3}$ a-p	1.51		
width protoloph	1.50		
width metaloph	1.04		

Range: The holotype comes from the Upper Oreodon Zone, 1 mile north of the Paul Zerbst Ranch, 8 miles north and 1.5 miles east of Harrison, by road, in the NW 1/4 of Sec. 35, T 33 N, R 56 W, Sioux County, Nebraska. Of the referred specimens, Amer. Mus. No. 5535 is from the Cedar Creek and U.S.N.M. No. 1946 from the Big Badlands, all of Middle Oligocene age. This species is therefore one of the earliest as well as one of the most primitive members of the genus.

Eumys brachyodus sp. nov.

(Fig. 61)

Holotype: Mus. Comp. Zool. No. 5069, lower jaw with M$\overline{1}$–$\overline{3}$ left.

The teeth are short in comparison with their width. M$\overline{1}$ has a small anteroconid, united with both the protoconid and the metaconid. On all the teeth there is a small mesoconid and no mesolophid. The lingual arm of the anterior cingulum is very short on M$\overline{2}$–$\overline{3}$, soon uniting with the protoconid and, after wear, giving the appearance of a tooth without any lingual half of the anterior cingulum. This is the easiest method of identifying this species. The posterior arm of the protoconids of M$\overline{2}$–$\overline{3}$ are closely related to the metaconids. In the last molar, the posterior arm of the protoconid diverges from the hypolophulid I instead of uniting with it buccally as in most members of the genus. The mandible is short, heavy and massive, sometimes extremely so, but sometimes at least the teeth are proportionately quite small. The incisor is usually quite heavy.

I have seen thirteen specimens referable to this species. Of these, ten are from the Upper Brulé of Nebraska, in the collections of the Museum of Comparative Zoology. The others are from uncertain levels, probably Oreodon Zone, in South Dakota and Colorado.

MEASUREMENTS OF *Eumys brachyodus*

	Holotype, Mus. Comp. Zool. No. 5069	*Mus. Comp. Zool. No. 5068*	*Mus. Comp. Zool. No. 5052*
	mm.	mm.	mm.
$M\bar{1}$–$\bar{3}$	6.85	6.88	6.51
$M\bar{1}$ a-p	2.36	2.32	2.10
width metalophid	1.71	1.43	1.47
width hypolophid	1.90	1.79	1.71
$M\bar{2}$ a-p	2.20	2.17	2.02
width metalophid	2.15	2.05	2.02
width hypolophid	2.12	2.04	2.09
$M\bar{3}$ a-p	2.15	2.40	2.24
width metalophid	2.00	2.10	1.99
width hypolophid	1.62	1.51	1.57

Eumys obliquidens sp. nov.

(Fig. 62)

Holotype: Amer. Mus. No. 5603, lower jaw with incisor and $M\bar{1}$–$\bar{3}$ right.

The posterior arm of the protoconid runs postero-mesiad and unites with the entoconid on $M\bar{2}$ and nearly does the same on $M\bar{3}$, resulting in a pattern that suggests the higher New World cricetids. At the same time, this species approaches closer to *Cricetodon* than does any other member of *Eumys* in that the mesolophid of $M\bar{1}$ is as long as or longer than the posterior arm of the protoconid. This is not, however, true of the other molars.

MEASUREMENTS OF *Eumys obliquidens*

	Holotype, Amer. Mus. No. 5603	*Amer. Mus. No. 5556*	*Amer. Mus. No. 5528*	*Amer. Mus. No. 5607*	*Univ. Nebr. No. 19–1–8–33–SP*	*Univ. Nebr. No. 2–15–7–33–SP*	*U.S. N.M. No. ——*
	mm.	mm.	mm.	mm.	mm.	mm.	mm.
$M\bar{1}$–$\bar{3}$	7.15	6.50	6.33	—	—	—	7.15
$M\bar{1}$ a-p	2.82	2.41	2.34	—	—	2.21	2.65
width metalophid	1.62	1.41	1.42	—	—	1.40	1.60
width hypolophid	1.88	1.68	1.65	—	—	1.71	1.94
$M\bar{2}$ a-p	2.23	2.13	2.02	2.31	2.28	2.17	2.23
width metalophid	2.11	1.90	—	—	2.10	1.82	2.09
width hypolophid	2.02	1.85	1.76	2.14	2.07	1.85	2.05
$M\bar{3}$ a-p	2.13	2.01	2.00	2.13	2.10	—	2.13
width metalophid	1.99	1.78	1.75	2.02	1.94	—	1.88
width hypolophid	1.36	1.39	1.24	1.44	1.58	—	1.35

As shown in the accompanying table, there is close agreement in size in the specimens referred to this species, though three of them are distinctly smaller than the others. Nevertheless, they are within the expectable size variation of a single species.

Range: The holotype is from the Cedar Creek Middle Oligocene Beds of Colorado. The other specimens come from the Oreodon Beds of Colorado, South Dakota and Nebraska.

Eumys exiguus sp. nov.[2]

(Figs. 63–64)

Holotype: Amer. Mus. No. 12,261, palate with M1–3 right and left and mandible with M$\bar{1}$–$\bar{3}$ left, apparently associated.

The cheek teeth are in an early stage of transformation from the typical *Eumys* type with transverse lophs to the type described below as characteristic of *Scottimus*, with antero-posterior lophs. The cross lophs of the upper molars are weakened, the mure is strongly developed, and a crest is growing across the median valley between the paracone and metacone. In the lower molars, the same process is taking place, the ectolophid being

MEASUREMENTS, *Eumys exiguus*

	Holotype, Amer. Mus. No. 12,261	*Princeton Univ. No. 11,385*	*Mus. Comp. Zool. No. 5068*
	mm	mm.	mm.
M1–3	5.82	—	—
M1 a-p	2.72	2.89	2.38
width anteroloph	0.92	1.29	—
width protoloph	1.74	1.89	1.68
width metaloph	1.70	1.74	1.66
M2 a-p	1.76	—	1.75
width protoloph	1.61	—	—
width metaloph	1.57	—	1.67
M3 a-p	1.35		
width protoloph	1.46		
width metaloph	1.10		
M$\bar{1}$–$\bar{3}$	5.92		
M$\bar{1}$ a-p	2.20		
width metalophid	1.20		
width hypolophid	1.46		
M$\bar{2}$ a-p	1.92		
width metalophid	1.57		
width hypolophid	1.63		
M$\bar{3}$ a-p	1.71		
width metalophid	—		
width hypolophid	1.22		

[2] The holotype of this species was identified with the above name in the American Museum collections by Dr. W. D. Matthew, who correctly recognized its distinction from *E. elegans* and its importance. Since, however, there is no manuscript of Dr. Matthew's dealing with this form, I must take the responsibility for the name upon myself.

very strong and subsidiary connections developing. In the upper teeth, the tendency is to form a large central basin, with peripheral crests, whereas in the lowers, the longitudinal crest is in the center of the tooth, and the valleys open outwards. The palatal foramina are much larger than is normal in *Eumys*, being a millimeter long and lying in large, deep pits.

Range: Middle Oligocene of South Dakota, the holotype being from the Middle Oreodon Beds of Sheep Mountain.

Scottimus gen. nov.[3]

Genotype: *Scottimus lophatus* n. sp.

The upper cheek teeth, with two antero-posterior crests, and the lower teeth, with one, represent the continuation of the trend illustrated by *Eumys exiguus*, with the further weakening of the ancestral lophs and continual emphasis on the mure, the ectolophid and the crest between the lingual margins of the paracone and metacone. M2–3 ultimately tend to lose all sign of the individual cusps, the teeth appearing as a crest of uniform elevation surrounding a large central basin. The lower teeth retain a rather primitive talonid, but the trigonid loses the primitive cross crests, and develops a more pronounced antero-posterior trend.

This genus is the most specialized of the Oligocene cricetids. The extreme modification of the pattern from that of the typical *Eumys*, through *E. exiguus* to the antero-posterior crest of *Scottimus lophatus* is quite clearly shown by the accompanying figures (Figs. 57 to 67). This pattern is quite aberrant, not appearing to be closely related to that of any other cricetids with which I am familiar.

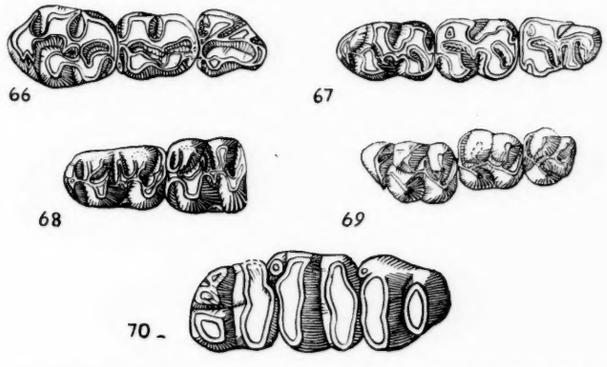

FIG. 66. *Scottimus lophatus* n. gen., n. sp. Diplotype. M.C.Z. No. 5064, M1–3 right.
FIG. 67. *Scottimus lophatus* n. gen., n. sp. U. Nebr. No. 75-3-7-33-SP, M1–3 right.
FIG. 68. *Cricetodon nebraskensis* n. sp. Holotype. U. Nebr. No. 8-4-8-33-SP, M1–2 left.
FIG. 69. *Leidymys vetus* n. sp. Holotype. Amer. Mus. No. 8742, M1–3 left.
FIG. 70. *Diplolophus insolens* Troxell. Diplotype. Y.P.M. No. 10,368, M1–3 right.
All figs. × 5.

[3] I wish to use the naming of this genus as an occasion for expressing my gratitude to Professor Scott for the opportunity which he has afforded me of reviewing the rodents and lagomorphs of the White River.

Scottimus lophatus sp. nov.

(Figs. 66–67)

Holotype: Mus. Comp. Zool. No. 5064, maxilla with M$\underline{1}$–$\underline{3}$ right.

Princeton Univ. No. 11,385, tentatively referred to this form, seems to be intermediate between *Eumys exiguus* and *Scottimus lophatus*, and probably represents a third form.

MEASUREMENTS OF *Scottimus lophatus*

	Holotype, Mus. Comp. Zool. No. 5064	*Princeton Univ. No. 11,385*
	mm.	mm.
M$\underline{1}$–$\underline{3}$	7.34	
M$\underline{1}$ a-p	3.12	
width protoloph	2.27	
width metaloph	2.04	
M$\underline{2}$ a-p	2.30	1.94
width protoloph	1.83	1.62
width metaloph	1.71	1.56
M$\underline{3}$ a-p	2.00	1.54
width protoloph	1.79	1.34
width metaloph	1.71	1.18
M$\overline{1}$–$\overline{3}$	7.48	
M$\overline{1}$ a-p	2.77	
width metalophid	1.63	
width hypolophid	1.68	
M$\overline{2}$ a-p	2.37	
width metalophid	1.80	
width hypolophid	1.72	
M$\overline{3}$ a-p	2.33	
width metalophid	1.70	
width hypolophid	1.37	

Horizon: Upper Brulé of Morrill County, Nebraska. The holotype is from Chimney Rock, below the upper ash, at an elevation of 4000 feet.

Cricetodon Lartet

Cricetodon nebraskensis sp. nov.

(Fig. 68)

Holotype: U. Nebr. No. 8–4–8–33–SP, one of three jaws with this number, containing M$\overline{1}$–$\overline{2}$ left.

This genus is the characteristic cricetid of the Old World, and especially European, Tertiary. In view of the extreme prevalence of the *Eumys*-type of teeth in the New World cricetids, it is quite interesting to find a typical *Cricetodon* here. The genus may readily be told from the American forms by the long mesolophid, which is definitely longer than the posterior arm of the protoconid on both M$\overline{1}$ and M$\overline{2}$. This may readily be observed

by comparing the figures of *Eumys* and *Cricetodon* in the plates of Schaub's monograph (1925).

The only American specimen that I have seen falling within the limits of this genus is the specimen listed above as the holotype of *C. nebraskensis*.

MEASUREMENTS OF *Cricetodon nebraskensis*

	Holotype, Univ. Nebr. No. 8–4–8–33–SP		*Holotype, Univ. Nebr. No. 8–4–8–33–SP*
M1 a-p	2.83 mm.	M2 a-p	2.24 mm.
width metalophid	1.57 mm.	width metalophid	2.08
width hypolophid	1.79	width hypolophid	2.08

Range: Upper Oreodon Beds, 1 mile N. of Paul Zerbst Ranch, 10 miles north of Harrison, Sioux County, Nebraska.

Leidymys Wood 1936

This genus may be identified as a *Eumys*-like cricetid with the temporal crests widely separated, the upper part of the infra-orbital foramen larger proportionately than in *Eumys*, and the lower part smaller. The snout is very slender, as contrasted with the conditions in *Eumys* (see above, p. 247). The upper incisors are narrow with an almost flat face, instead of being wide as in *Eumys*. M3 has a small protocone and a large hypocone. The cheek teeth are more slender than in *Eumys*.

Leidymys vetus sp. nov.

(Fig. 69)

Holotype: Amer. Mus. No. 8742, antorbital portion of the skull with M1–3 right and left.

This species differs from the John Day members of the genus in having a larger protocone and a smaller hypocone on M3—that is, in approaching more nearly to the conditions as found in *Eumys*. In the upper incisors, there is no trace of the ridges that characterize *L. lockingtonianus*. The separation of the temporal crests and the complete absence of a sagittal crest might be considered as being either age or sexual characters were it not that this is the only specimen from the White River that shows such characters, even though there are numerous other known specimens just as young as this animal. As I have pointed out before, it would be extremely surprising if all the other known cricetid skulls from the White River deposits were males, with this one the single female. The chances against this are so large that it may be safely neglected.

As would be expected, the White River *Leidymys* is much nearer the White River *Eumys* than is the John Day *Leidymys*. In fact, I would never consider that *L. vetus* is sufficiently distinct from *Eumys* to warrant generic separation. On the other hand, it is even closer to the John Day species, which, in turn, are clearly generically distinct from *Eumys*. This, of course, is merely another illustration of the fact that when all stages in an evolutionary sequence are known, it is impossible to draw hard and fast lines at any point.

MEASUREMENTS OF *Leidymys vetus*

	Holotype, Amer. Mus. No. 8742		*Holotype, Amer. Mus. No. 8742*
M1–3	6.02 mm.	M2 a-p	1.83 mm.
M1 a-p	2.69	width protoloph	1.67
width anteroloph	1.26	width metaloph	1.54
width protoloph	1.72	M3 a-p	1.49
width metaloph	1.72	width protoloph	1.64
		width metaloph	1.19

Horizon: Middle Oligocene Cedar Creek Beds of Colorado.

RODENTIA Incertae Sedis

Diplolophus is a very difficult rodent to place taxonomically. Troxell (1923) completely avoided all mention of its supergeneric position, though his uniting *D. insolens* with *D. parvus*, a heteromyid (*Proheteromys parvus*), may indicate that he thought it had heteromyid affinities. Hay (1930, p. 873) apparently realized that *D. insolens* could not be a heteromyid, and placed it among the Sciuridae, where it is even more out of place than among the Heteromyidae. The most obvious similarity of the cheek teeth is to the geomyoids. In this fossil, however, there are only three teeth, and the details of the pattern are different from anything within the geomyoids. If *Diplolophus* should by any chance be a geomyoid, it must represent either an aberrant individual or an aberrant line, in which either the first or the second molar has been lost. The jaw does not seem to be that of a geomyoid. Needless to say, there is no possibility that the teeth are dP$\overline{4}$–M$\overline{2}$. If this rodent is not a geomyoid, I can think of no other group with which it could possibly be associated.

Diplolophus Troxell

(Fig. 70 and Troxell, 1923, Figs. 1–2)

Genotype: *D. insolens* Troxell 1923.

The cheek teeth are bilophodont as in the geomyoids, with an apparently similar tooth pattern; only three teeth in the lower jaw in the type and only known specimen, which is an adult. The first tooth has a pattern like that of P$\overline{4}$ in geomyoids, and quite different from their M$\overline{1}$. The last tooth appears like M$\overline{3}$ of geomyoids. The jaw is massive, the masseteric fossa ending below M$\overline{1}$.

The anterior loph of M$\overline{1}$ is composed of a main lingual cusp and two smaller, closely appressed, buccal ones. The hypolophid seems to be formed of three cusps, but the valleys separating them are shallow, and have been destroyed by wear. M$\overline{2}$–$\overline{3}$ both show three main divisions in each loph. M$\overline{2}$ apparently has three cusps and an antero-external stylid in the metalophid (Fig. 70), and three cusps in the hypolophid. There seem to be but two cusps in each of these crests in M$\overline{3}$, in addition to the antero-external stylid of the metalophid.

The jaw is somewhat heavier in proportion than would be the case in a heteromyid or even an entoptychine. The masseteric crest extends as far forward as below M$\overline{1}$, ending

just posterad of the mental foramen. The mandibular foramen seems to have lain in the slight groove between $M\bar{3}$ and the coronoid process, a geomyoid character.

In its general superficial appearance, this form closely simulates the geomyoids. The most striking difference is the absence of one tooth which occurs in the latter. This is, of course, a difference frequently considered of sub-ordinal value among the rodents. The great narrowing of the hypolophid when compared with the metalophid in the last tooth of *Diplolophus* indicates that, if it is related to heteromyids, this tooth must be $M\bar{3}$. The detailed appearance of the protostylids of the last two teeth is quite different from their appearance in any of the Geomyoidea. The crests of the two posterior teeth are much more progressive and show much less indication of independent cusps than is the case among the Oligocene and Lower Miocene heteromyids and entoptychines, and the pattern is quite different from that of the Lower Miocene Geomyinae. If this form should be a geomyoid, the anterior tooth would of necessity be $P\bar{4}$. In this case, as the posterior one is $M\bar{3}$, one of the intermediate teeth must have been lost, a condition otherwise unknown, as far as I am aware, except among the Mylagaulidae, where the loss of the anterior molars is brought about by special conditions not operating in this instance.

It is therefore at present impossible to determine the relationships of this form. It may be a pathologic individual of one of several unknown or poorly known phyla of geomyoids. It may represent a new family of geomyoids which early lost the third molar and subsequently paralleled the other families as they have paralleled each other. Or it may represent an entirely distinct stock, belonging to the "Myomorph" group, which, after losing the premolar, developed dental similarities to the Geomyoidea. As suggested by Dr. G. E. Lewis (see Wood, 1935*b*, footnote, p. 371), there are certain interesting similarities to the Muridae in the pattern of *Diplolophus*, which may or may not be of significance.

Diplolophus insolens Troxell

Holotype: Y.P.M. No. 10,368, lower jaw with $M\bar{1}$–$\bar{3}$ right.

This is the only species which can at present be referred to the genus.

MEASUREMENTS OF *Diplolophus insolens*

	Holotype, Y.P.M. No. 10,368		*Holotype, Y.P.M. No. 10,368*
$M\bar{1}$ a-p	2.46 mm.	$M\bar{3}$ a-p	1.95 mm.
width metalophid	2.27	width metalophid	2.61
width hypolophid	2.50	width hypolophid	1.89
$M\bar{2}$ a-p	2.36		
width metalophid	2.87		
width hypolophid	2.72		

Horizon: Middle Oligocene Oreodon Beds of Nebraska.

CONCLUSIONS

Having now completed this detailed review of the rodents of the White River, it would be well to summarize the general results. One striking feature is the large number of forms present, representing at least nine families, whereas there are but nine living in North America at present. The nineteen fossil genera are, of course, distinctly less numerous than the seventy-five recent ones.

Of the recent families, only four are represented in the White River. In addition, the zapodids seem to have existed in North America at this time (Wilson, 1935), while the sciurids were probably extant here, in view of their presence in the John Day. It is an interesting commentary, however, that the Sciuridae, commonly supposed to be one of the most primitive of rodent families, are among the latest of the families now present in North America to have made their appearance. A third Recent North American family not found in the White River are the erethizontids, a relatively recent South American invasion. They are, of course, known from the Oligocene of Patagonia. The Aplodontidae appear to have originated in North America about Oligocene time. The Muridae, of course, were introduced by Man.

This leads to one of the most striking features of rodent palaeontology—the sharp break between the Recent and what may be called the Eocene families of rodents. As has been indicated above, of the nine families recognized in the White River, four continue to the present. Not one of these has any ancestor known earlier than the Oligocene, and, with the exception of a badly worn specimen referred to *Agnotocastor*, no traces of them are known before the Brulé. Four of the other families can be traced up from Eocene ancestors, but, with the exception of the possible sciuravid *Kansasimys* from the Pliocene (Wood, 1936*c*), no members of these families are known later than the Oligocene, and none of them have any known descendants, though the aplodontoids are probably collateral relatives of the ischyromyids. The other two groups, the Eutypomyidae and *Diplolophus*, have neither known ancestors nor descendants.

Since the White River has thus been shown to be the crossroads where the modern and the primitive types of rodents interdigitate, it is particularly important that much further work should be done to elucidate these relationships. It is therefore very gratifying that these deposits should be as extraordinarily rich in fossil rodents as they are. Of course, it is quite probable that further work will not find any relationships between these two groups of White River rodent families, but will result in the discovery of the modern group in earlier and earlier beds, and of the other forms in later and later ones. In fact, if the "Sciuromorpha" and "Myomorpha" are natural groups, I do not see how they could have separated from the "Protrogomorpha" later than the Middle Eocene. If they should turn out not to be natural groups, the whole matter becomes so exceedingly complicated that absolutely nothing can be made of it at the present time.

In summary, it might be well to give a brief outline of my present views as to the classification of the rodents, based on the material that has been studied in connection with this or other recent works on fossil rodents. The only groups that I am including in this

outline are those that I have personally had some opportunity to study, so that as a result the classification is naturally quite incomplete. It may, however, help to furnish a basis for discussion of the numerous difficult and unsolved problems of rodent taxonomy. The groups listed below do, moreover, include most of the North American rodents, as well as some others.

Order Rodentia Vicq d'Azyr, 1792
- Suborder Protrogomorpha Zittel, 1893
  - Superfamily Ischyromyoidea
    - Family Paramyidae Miller and Gidley, 1918
    - Family Sciuravidae Miller and Gidley, 1918
    - Family Ischyromyidae Alston, 1876
    - Family Cylindrodontidae Miller and Gidley, 1918
    - Family Protoptychidae, new family
  - Superfamily Aplodontoidea Matthew, 1910
    - Family Allomyidae Marsh, 1877
    - Family Aplodontidae Trouessart, 1904
    - Family Mylagaulidae Cope, 1881
- Suborder "Sciuromorpha" Brandt, 1855
  - Superfamily Sciuroidea Gill, 1872
    - Family Sciuridae Gray, 1821
  - Superfamily Geomyoidea
    - Family Heteromyidae Allen and Chapman, 1893
    - Family Geomyidae Bonaparte, 1850
  - Superfamily Castoroidea Gill, 1872
    - Family Castoridae Gray, 1821
    - Family Eutypomyidae Miller and Gidley, 1918
  - Incertae Sedis
    - Family Eomyidae Deperet and Douxami, 1902
- Suborder "Myomorpha" Brandt, 1855
  - Superfamily Myoidea Gill, 1872
    - Family Cricetidae Rochebrune, 1883
    - Family Dipodidae Waterhouse, 1842
    - Family Sicistidae
    - Family Zapodidae Coues, 1876

It is, of course, true that there is no evidence that the superfamilies listed under the "Sciuromorpha" have any real relationship to each other. Neither is there any evidence that the superfamilies of "Myomorphs" have any significant relationship or that the families listed above under the Myoidea are related to the Muridae.

I think one of the best summaries of the whole problem of rodent classification was made by Forsyth Major. "For at the bottom of the whole matter, and the cause of all the mischief, are the hard-and-fast divisions into which the Rodent genera are up to the present day being forced. If we continue to cling to the 'time-honored' but unnatural sub-orders *Sciuromorpha, Myomorpha,* and *Hystricomorpha* of Brandt, we cannot hope to gain an insight into the mutual affinities of the various groups of the order. These sub-

STRATIGRAPHICAL AND GEOGRAPHICAL DISTRIBUTION OF WHITE RIVER RODENTS

	Pipestone Springs	Thompson Creek	Beaver Divide	Horsetail Creek	Titanotherium Beds	Cypress Hills	McCarty Mt.	Oreodon Beds	Cedar Creek	Cook Ranch	Pipestone Upper Beds	White Buttes	Leptauchenia Beds
Prosciurus vetustus	×				×								
P. relictus								×	×				?
P. saskatchewaensis						×		?	?				
P. aff. *lohiculus*						×							
? *P. jeffersoni*	×												
Ischyromys typus	?						1.	×	×				?
I. pliacus	×	×						×	×				×
I. troxelli								×	×				
I. parvidens						×		×	×				
Titanotheriomys veterior	×	×			?	?	1.	?					
T. wyomingensis			×										
Cylindrodon fontis	×	×			?	×	1.						
Cylindrodon n. sp.			×	×									
Pseudocylindrodon neglectus	×												
? *Sespemys* sp.													×
Heliscomys vetus									×				
H. gregoryi										×			
H. senex								×					
H. hatcheri								×					
Proheteromys nebraskensis													×
Gidleumys adspectans								×					
Agnotocastor praetereadens					?			?					×
A. montanus								×					
Eutypomys thomsoni								×					
E. parvus						×							
E. magnus					?			×					
Eutypomys sp.		×											
Adjidaumo minutus								×	×				
A. minimus	×												
A. douglassi												×	
Paradjidaumo minor	×							?					
P. trilophus								×	×				
Eumys elegans								×	×	×	×		×
E. parvidens								×	×				
E. brachyodus								×	×				×
E. obliquidens								×	×				
E. exiguus								×					
Scottimus lophatus								×					×
Cricetodon nebraskensis													
Leidymys vetus									×				
Diplolophus insolens								×					

[1] Fide Douglass, 1906.

Since this chart was prepared, Burke has described *Ardynomys occidentalis* from the McCarty Mountain Beds.

orders are unnatural because (1) they ignore the fossil Rodentia and the lessons taught by them; (2) in some instances they present an amalgamation of heterogeneous groups; and (3) they draw barriers where in reality there are none. Winge, by pulling down these artificial barriers, has taken the bull by the horns, and we cannot do better than follow him." (Major, 1899, pp. 500–501.) It is somewhat difficult to determine just exactly what Winge's ideas on classification were. He was certainly twenty years ahead of everyone else (except, it would seem, Forsyth Major) in his realization of the extreme complexity of the subject and the unsatisfactory nature of the standard classifications. In many respects, the classification suggested above is very similar to that of Winge (1887). The chief point in which I differ with him is in the relationships of the ischyromyoids with *Aplodontia*, which, in view of the lack of knowledge of the former group in Winge's time, is not surprising.

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EXPLANATIONS OF THE PLATES

PLATE XXIII

Fig. 1. *Prosciurus* aff. *saskatchewaensis*, cranium, top view, × 2, Amer. Mus. Nat. Hist. No. 1429.
Fig. 1*a*. *Prosciurus* aff. *saskatchewaensis*, occiput, × 2, Amer. Mus. Nat. Hist. No. 1429.
Fig. 1*b*. *Prosciurus* aff. *saskatchewaensis*, cranium, base, × 2, Amer. Mus. Nat. Hist. No. 1429.
Fig. 2. *Prosciurus relictus*, lower jaw, side, × 2, Mus. Comp. Zool., Harvard, No. 6181.
Fig. 3. *Ischyromys troxelli*, holotype, ventral view of zygomatic plate, × 2, Amer. Mus. Nat. Hist. No. 12,248.
Fig. 4. *Prosciurus vetustus*, holotype, anterior view of zygomatic plate, × 4, Amer. Mus. Nat. Hist. No. 9626.
Fig. 5. *Ischyromys* sp., dorsal view of brain cast, × 2, A. E. Wood, No. 221.
Fig. 6. *Ischyromys typus*, right side of sacrum, × 2, Amer. Mus. Nat. Hist. No. 12,249.
Fig. 7. *Ischyromys typus*, left side of pelvis, × 2, Amer. Mus. Nat. Hist. No. 12,249.

PLATE XXIV

Cylindrodon sp., Amer. Mus. Nat. Hist. Nos. 14,584 and 14,585

Jaw from *C. fontis*, composite of Amer. Mus. Nat. Hist. Nos. 9639 and 9649

Fig. 1. Skull, left side.
Fig. 1*a*. Skull, base.
Fig. 1*b*. Skull, top.
All figures × 4.

The plate of the skull of *Ischyromys* was inadvertently omitted. It will be included with the plates of the Lagomorpha in a later part of this review.

PLATE XXV

Ischyromys typus

Fig. 1. Right scapula.
Fig. 1*a*. Right scapula, distal view of glenoid cavity.
Fig. 2. Right clavicle.
Fig. 3. Left humerus, front.
Fig. 3*a*. Left humerus, external side.
Fig. 4. Right radius, front.
Fig. 5. Right ulna, front.
Fig. 6. Right femur, front.
Fig. 6*a*. Right femur, posterior side of proximal end.
Fig. 7. Right patella, front.
Fig. 7*a*. Right patella, rear.
Fig. 8. Part of right pes, dorsum.
Fig. 9. Atlas, front view.
Fig. 9*a*. Atlas, dorsal side.

Fig. 10. Axis, dorsal side.
Fig. 10*a*. Axis, left side.
All figures × 2.
All figures from Amer. Mus. Nat. Hist. Figs. 2–5 and 7 from No. 1414. Figs. 1 and 6 composites of Nos. 1414 and 12,247. Figs. 9–10 from No. 12,247. Fig. 8 from No. 9721.

PLATE XXVI

Ischyromys typus

Skeleton, from the left, × 2/3, composite of Amer. Mus. Nat. Hist. Nos. 1414, 12,247 and others.

PLATE XXVII

Titanotheriomys veterior

Fig. 1. Skull, left side, Amer. Mus. Nat. Hist. No. 14,579.
Fig. 1*a*. Skull, base, Amer. Mus. Nat. Hist. No. 14,579.
Fig. 1*b*. Skull, top, Amer. Mus. Nat. Hist. No. 14,579.
Fig. 2. Left tibia and fibula, front, Amer. Mus. Nat. Hist. No. 12,247.
Fig. 3. Calcaneum, distal end, Amer. Mus. Nat. Hist. No. 9659.
Fig. 3*a*. Calcaneum, dorsal side, Amer. Mus. Nat. Hist. No. 9659.
Fig. 4. Astragalus, plantar side, Amer. Mus. Nat. Hist. No. 9659.
All figures × 2.

PLATE XXVIII

Agnotocastor praetereadens

Fig. 1. Skull, left side.
Fig. 1*a*. Skull, top.
Fig. 1*b*. Skull, base.
All figures × 2.
Amer. Mus. Nat. Hist. No. 1428. Jaw, Amherst No. 22–551.

PLATE XXIX

Eutypomys thomsoni

Fig. 1. Skull, left side.
Fig. 1*a*. Skull, base.
Fig. 1*b*. Skull, top.
All figures × 2.
Amer. Mus. Nat. Hist. No. 12,254.

PLATE XXX

Eutypomys thomsoni

Fig. 1. Left calcaneum, dorsal side.
Fig. 2. Left pes, dorsal side.
Fig. 2*a*. Left pes, fibular side.
Fig. 3. Right humerus, front.
Fig. 3*a*. Right humerus, external side.
Fig. 4. Left tibia, external side of proximal end.
Fig. 4*a*. Left tibia, posterior side of proximal end.
Fig. 5. Left tibia, distal end.
Fig. 6. Left astragalus, plantar side.
Fig. 7. Cervical vertebrae 6 and 7, dorsal vertebra 1, left side.

Fig. 8. Anterior dorsal vertebrae, left side.
Fig. 9. Posterior dorsal vertebrae, left side.
All figures × 2.
Figs. 1, 2, 4–6 from Amer. Mus. Nat. Hist. No. 12,255, Figs. 3, 7–9 from Amer. Mus. Nat. Hist. No. 12,254.

PLATE XXXI

Fig. 1. *Eutypomys thomsoni*, inner side of mandible, × 2, Amer. Mus. Nat. Hist. No. 12,254.
Fig. 2. *Eutypomys thomsoni*, dorsal view of brain cast, × 2, Amer. Mus. Nat. Hist. No. 1423.
Fig. 3. *Eumys parvidens*, holotype, skull, left side, × 4, U. Nebr. No. 22–1–8–33–SP.
Fig. 3*a*. *Eumys parvidens*, holotype, skull, base, × 4, U. Nebr. No. 22–1–8–33–SP.
Fig. 4. *Paradjidaumo minor*, skull, base, × 4, A. E. Wood, No. 9111.
Fig. 4*a*. *Paradjidaumo minor*, skull, left side, × 4, A. E. Wood, No. 9111.

PLATE XXXII

Eumys elegans

Fig. 1. Skull, left side.
Fig. 1*a*. Skull, base.
Fig. 1*b*. Skull, top.
All figures × 4.
Drawings from specimens in the Amer. Mus. Nat. Hist. and in the collection of Mr. Paul McGrew.

PLATE XXXIII

Eumys

Fig. 1. Skull, left side.
Fig. 1*a*. Skull, top.
Fig. 1*b*. Skull, base.
All figures × 4.
Amer. Mus. Nat. Hist. No. 1430.

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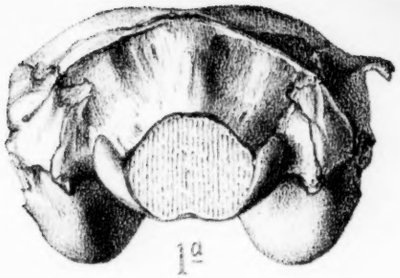

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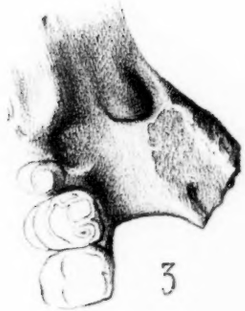

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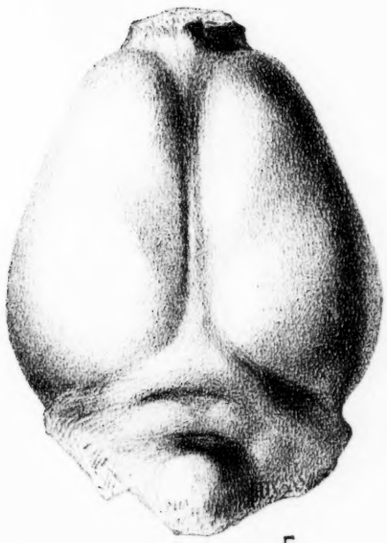

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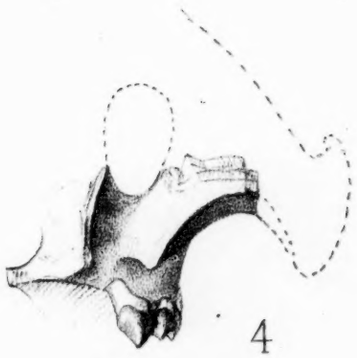

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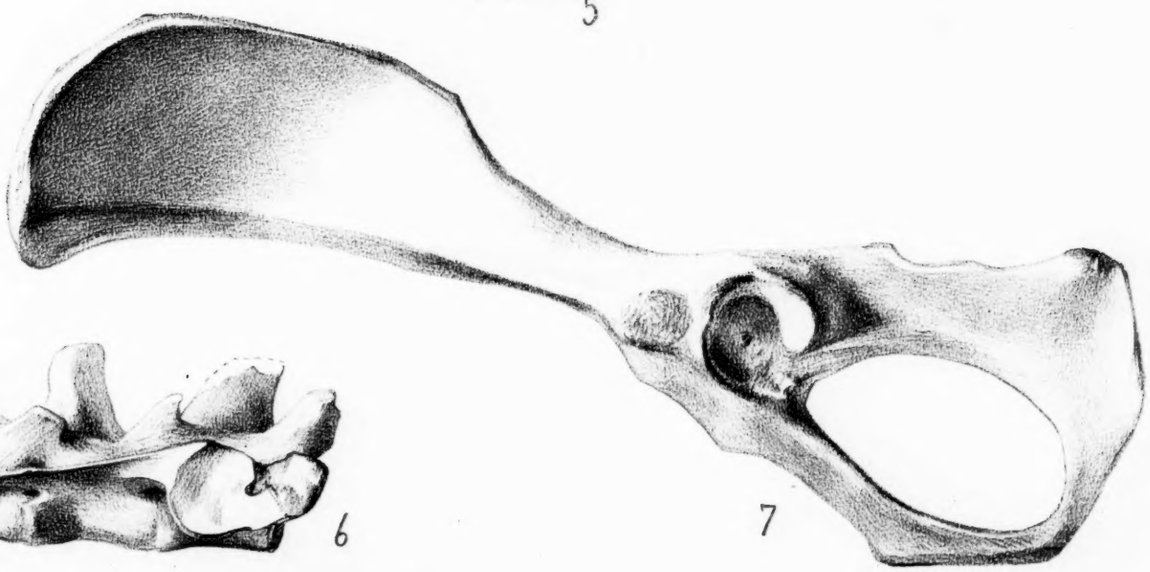

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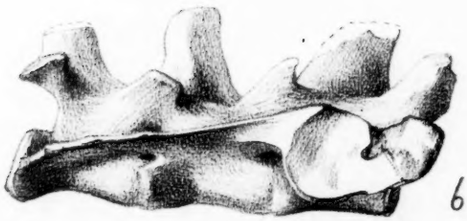
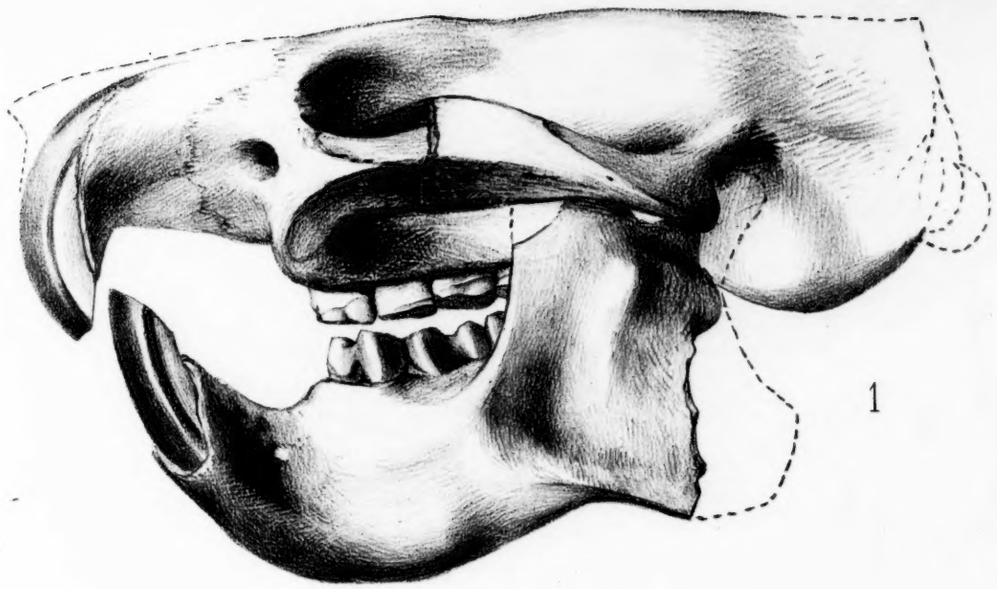


6

PROSCIURUS, ISCHYROMYS

COCKAYNE BOSTON



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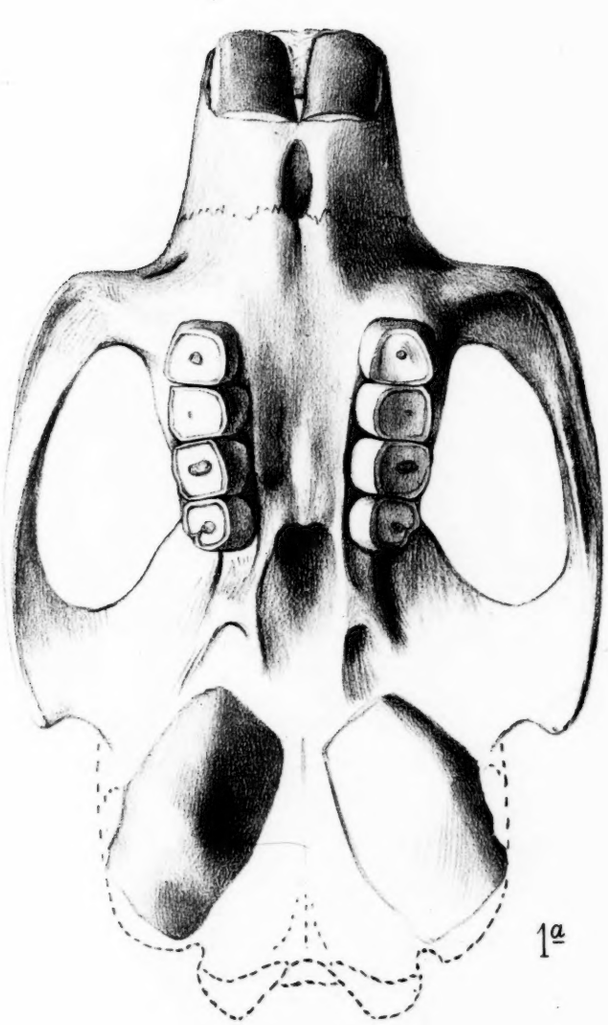

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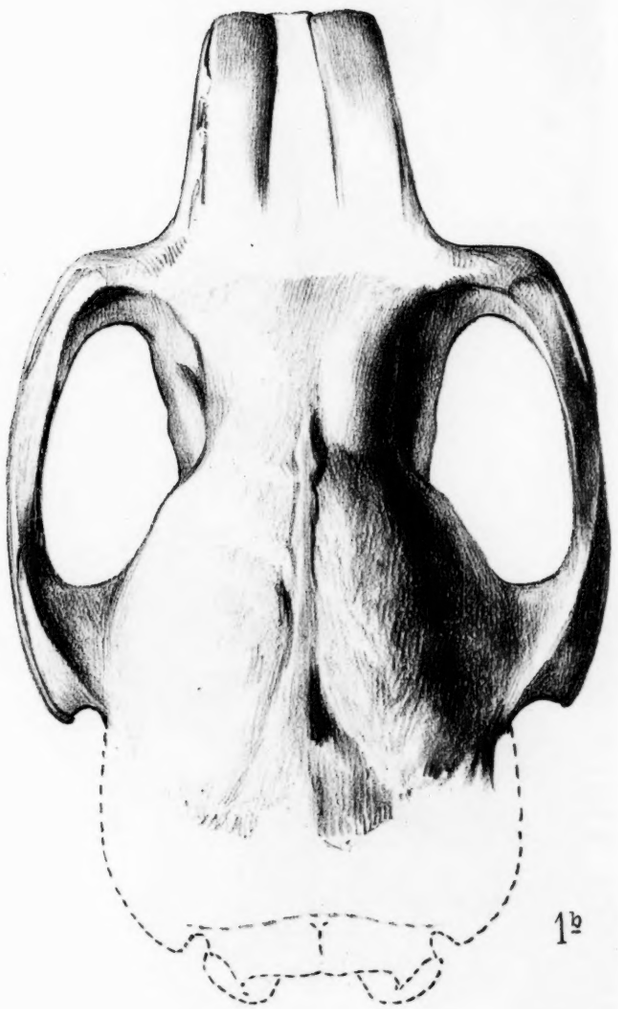

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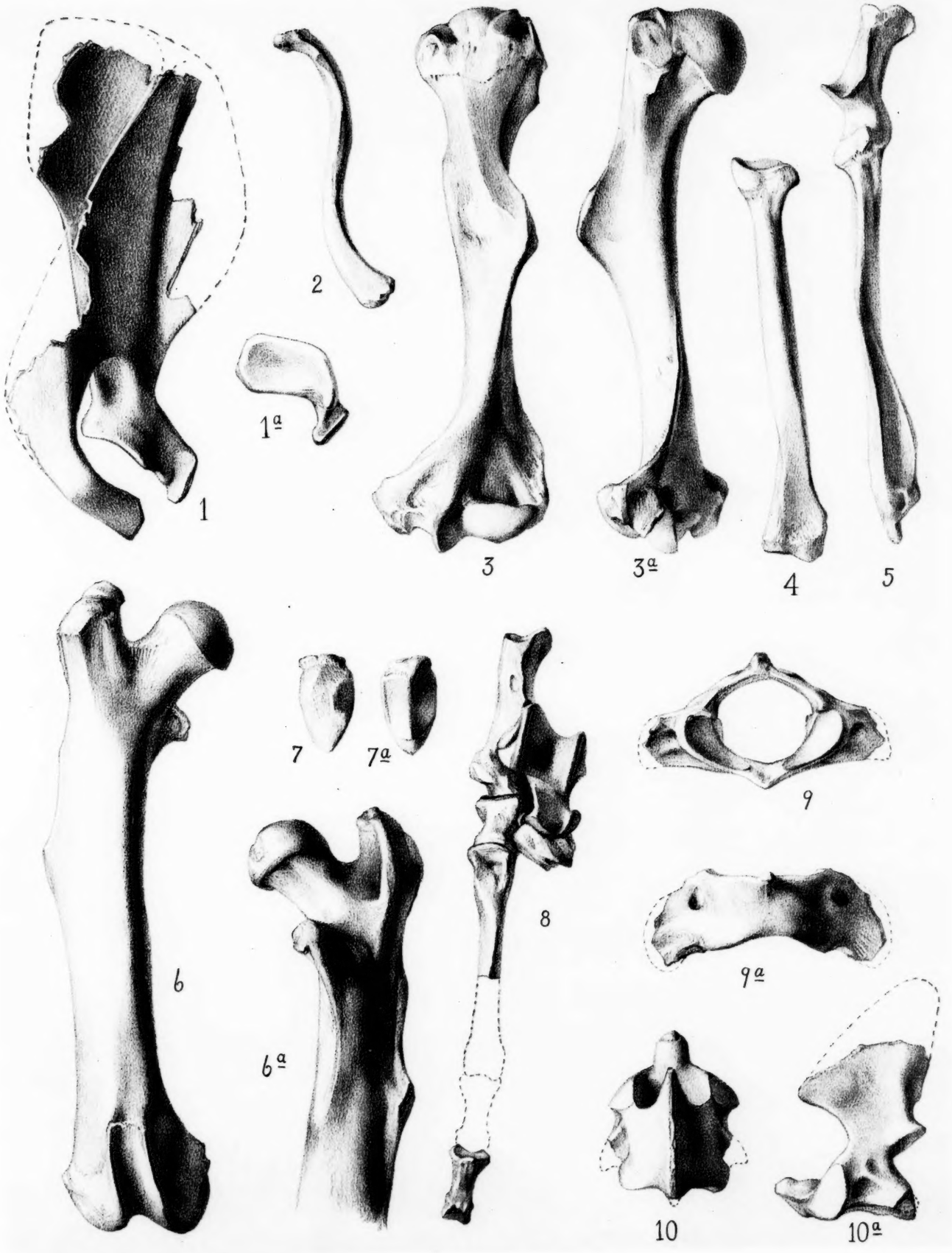

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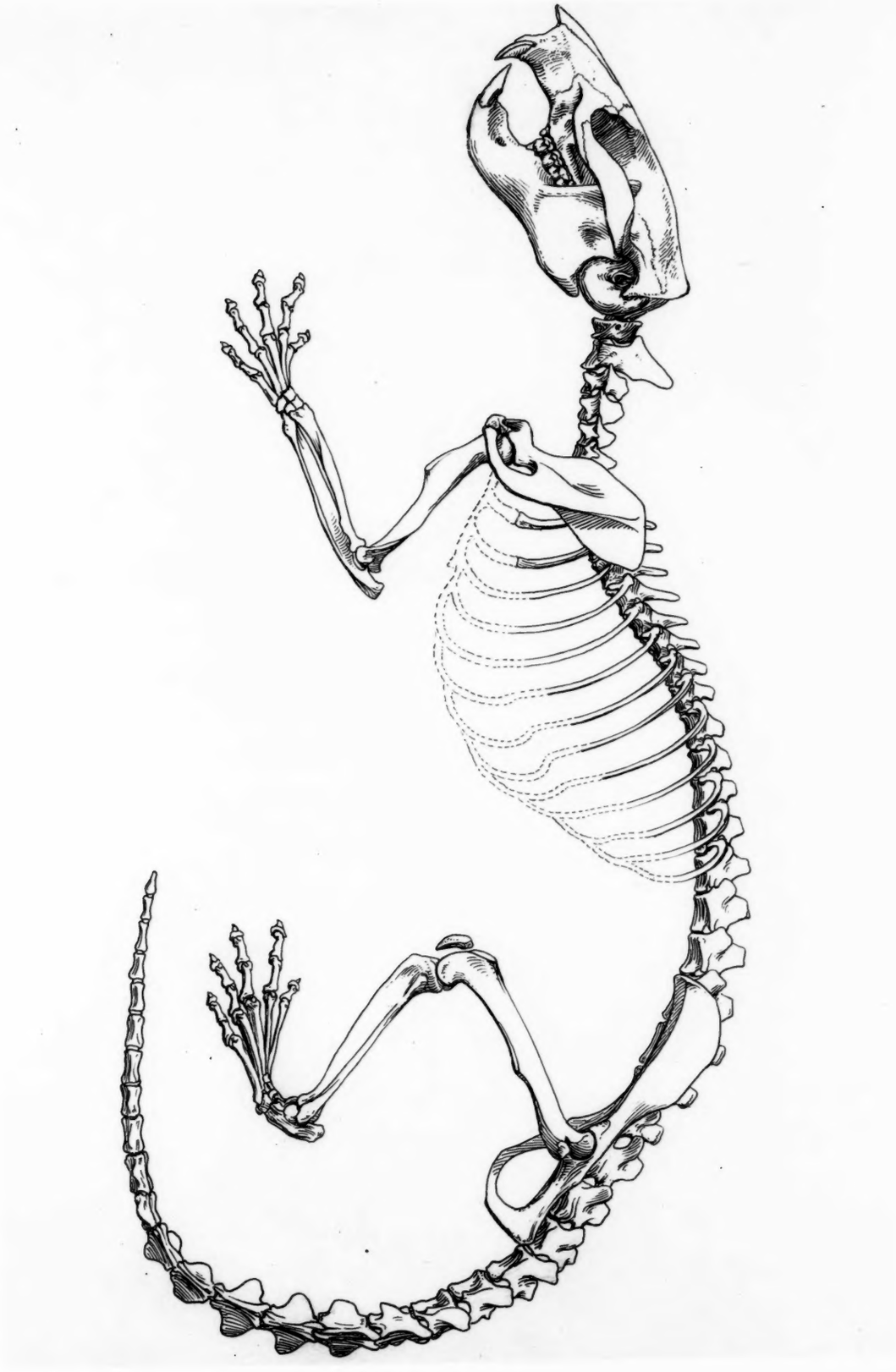

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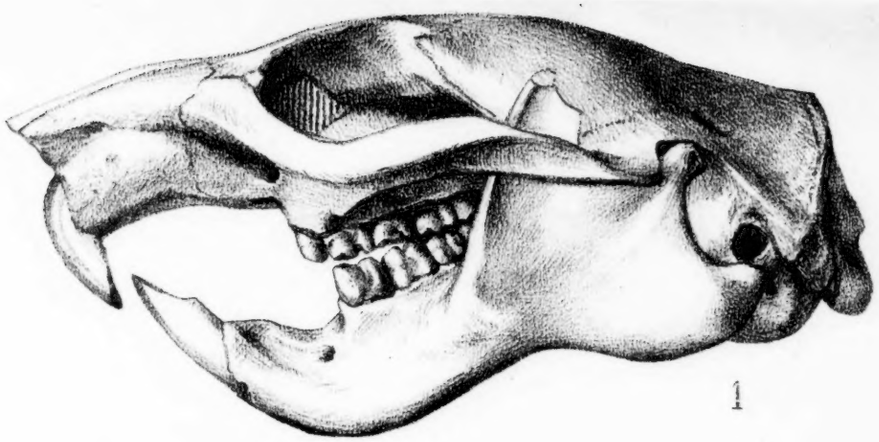

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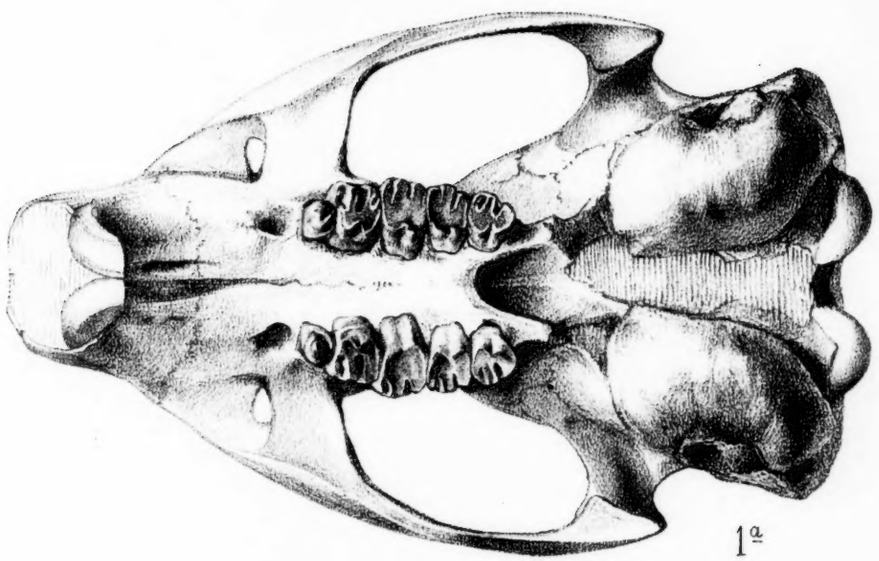

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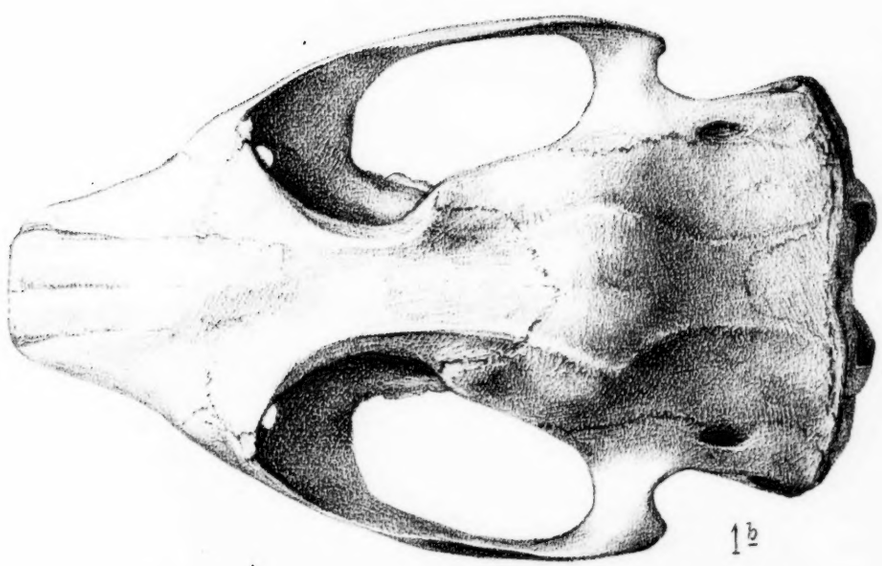

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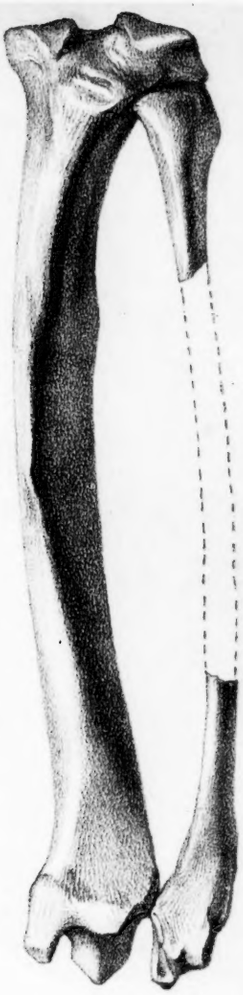

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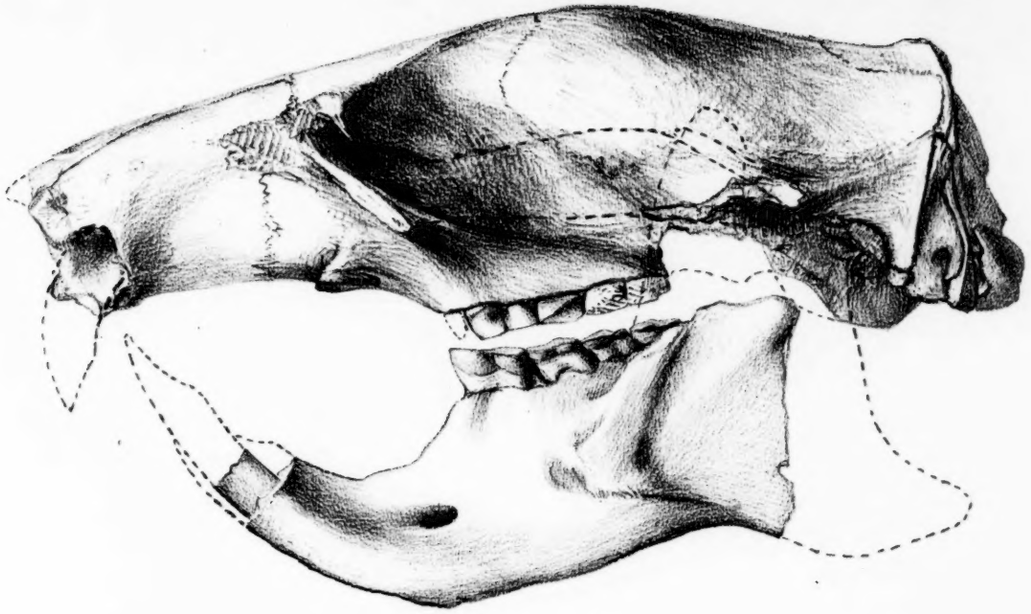
TITANOTHERIOMYS



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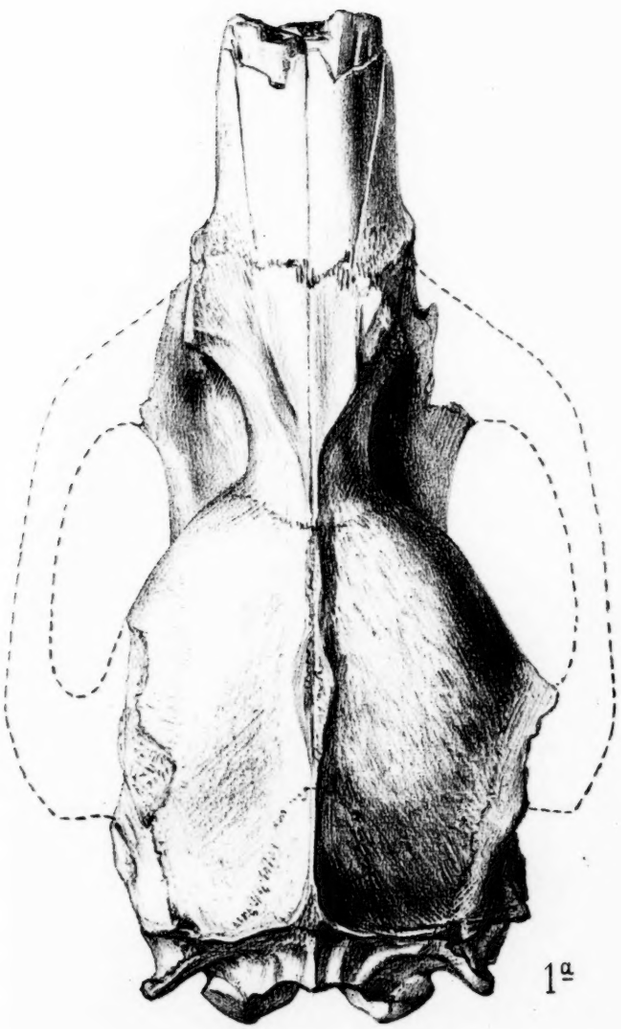

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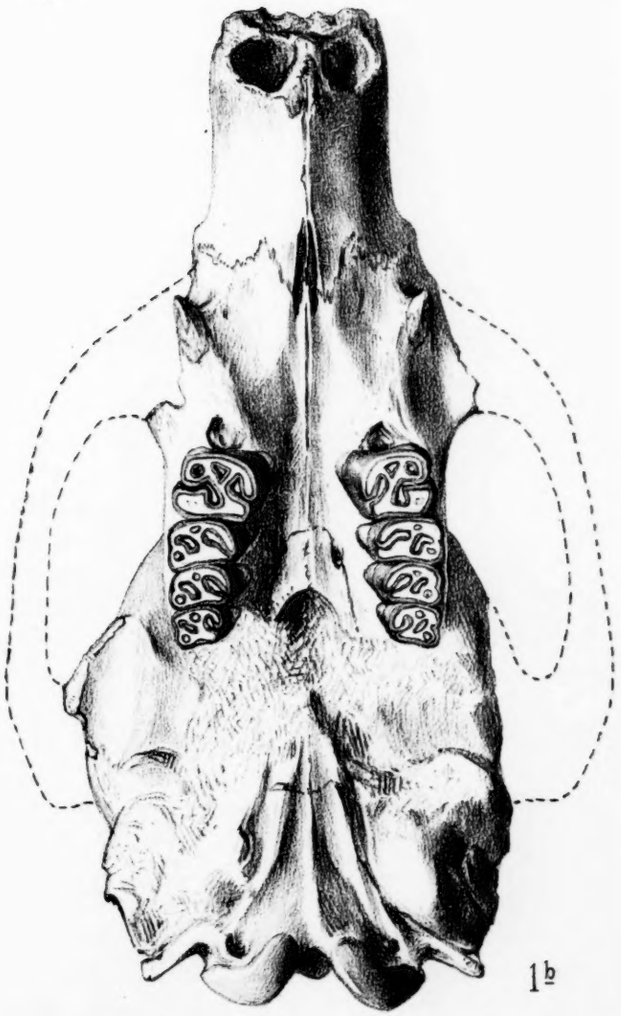

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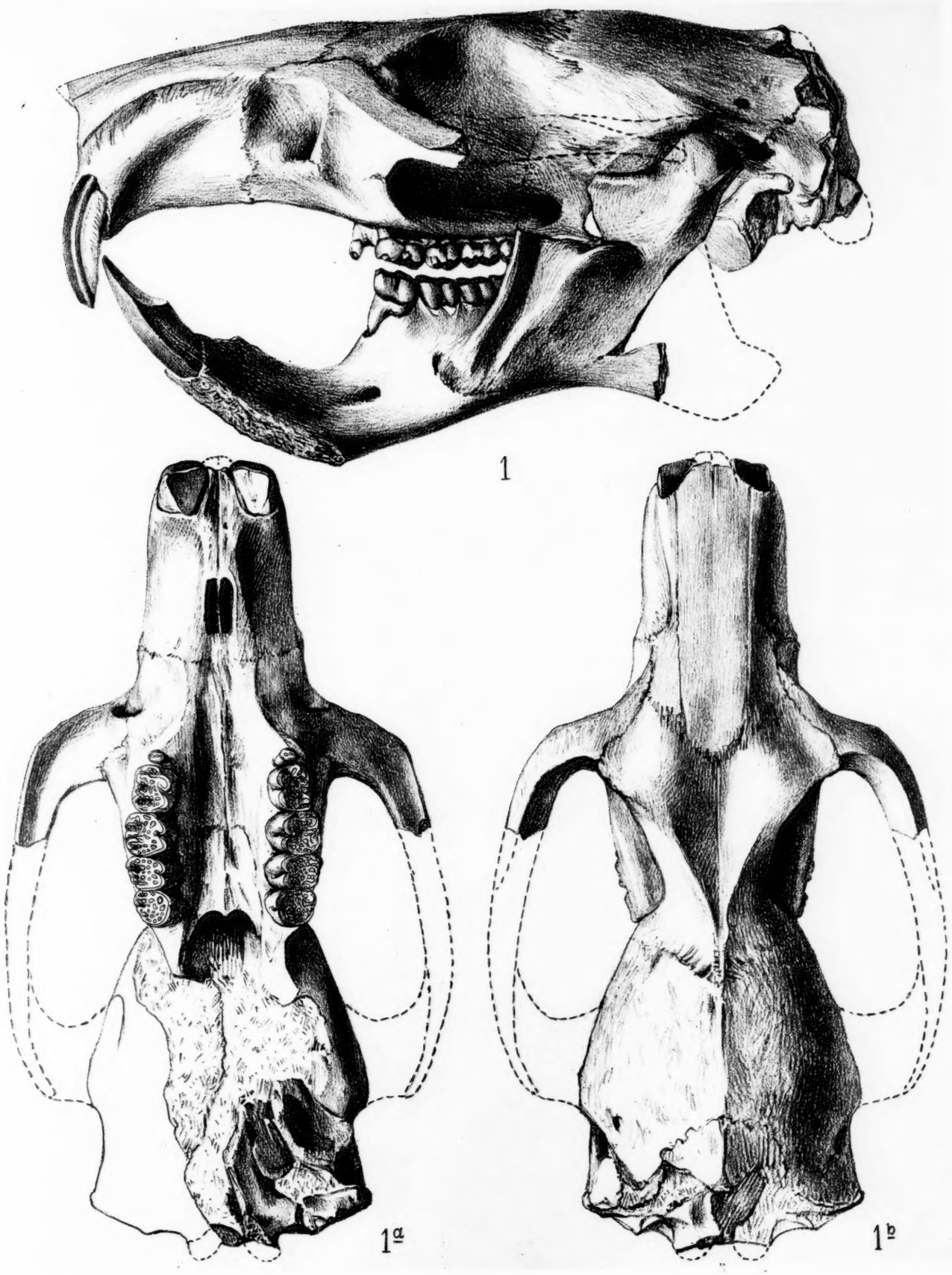

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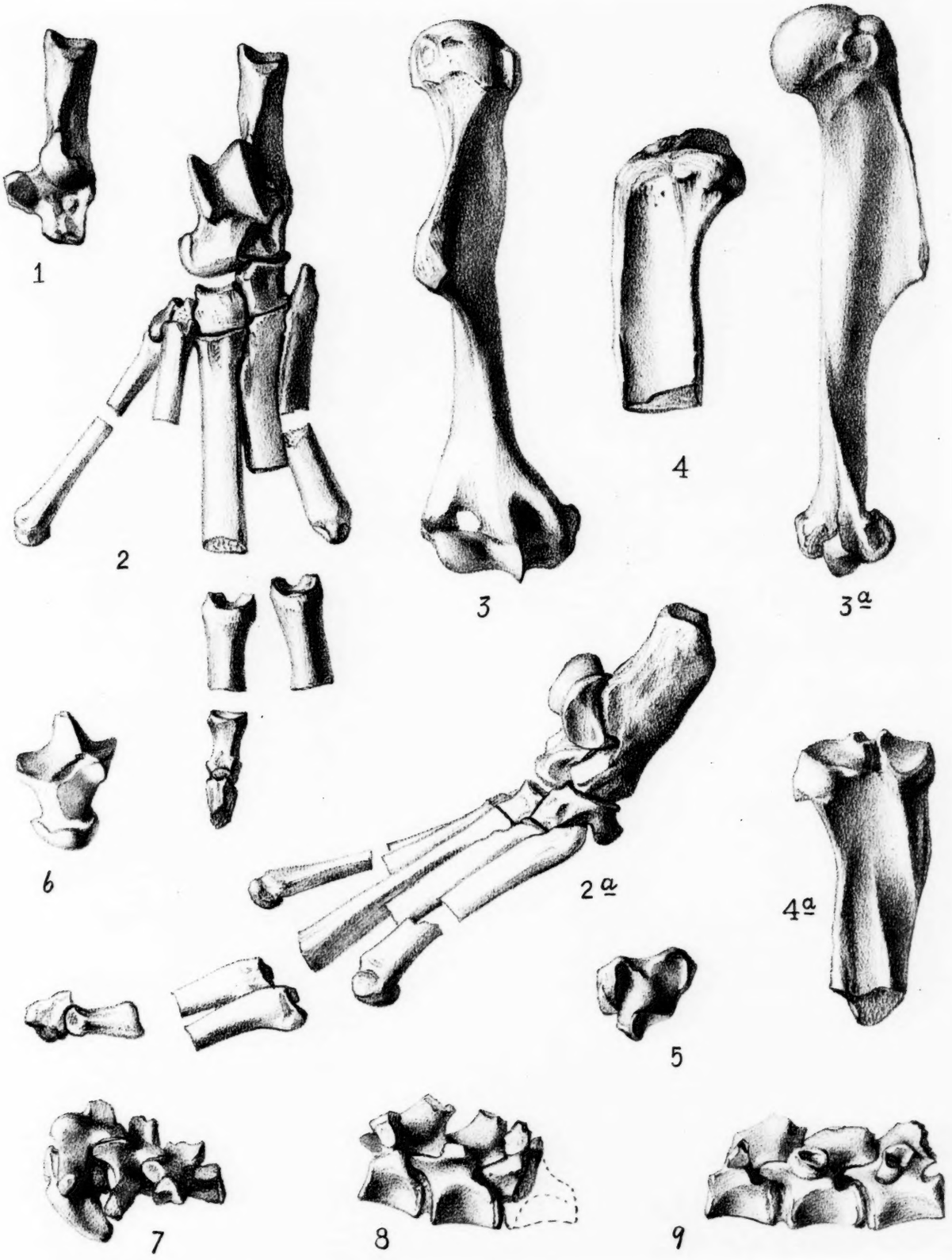

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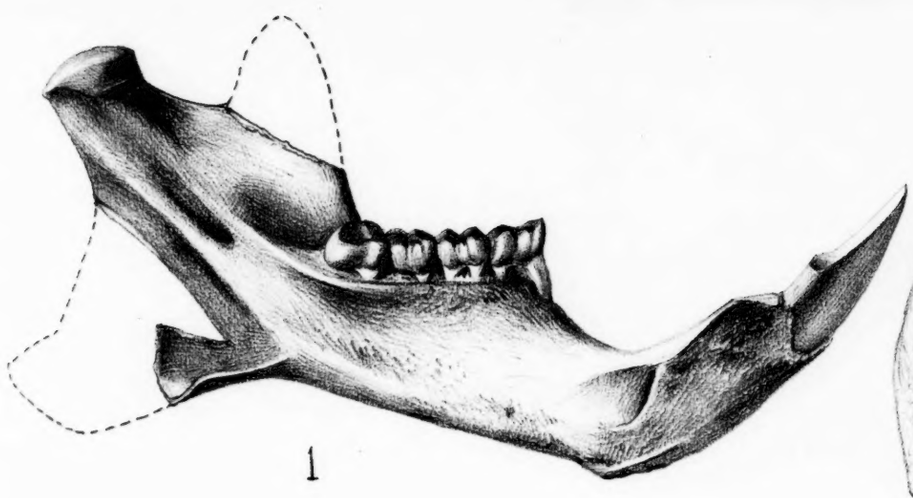

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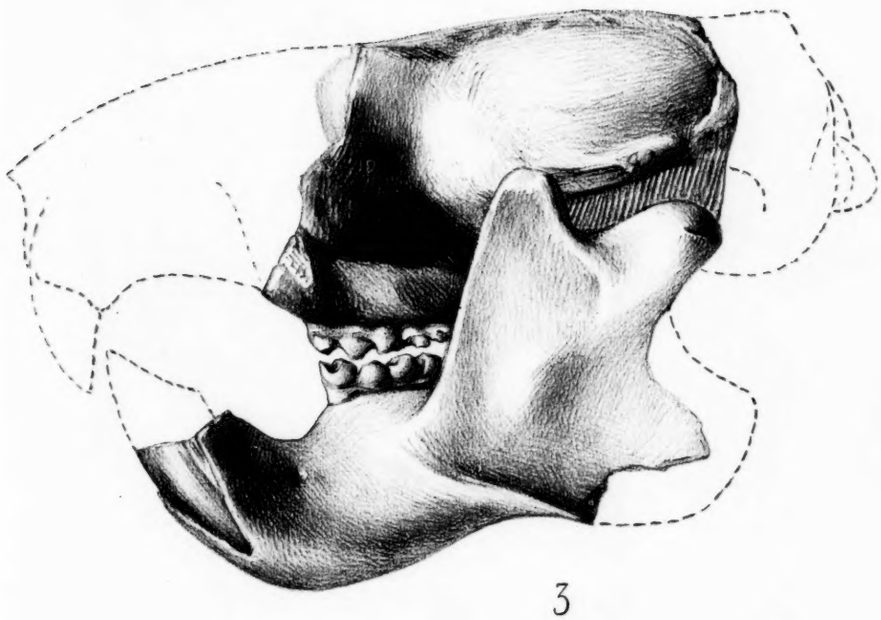

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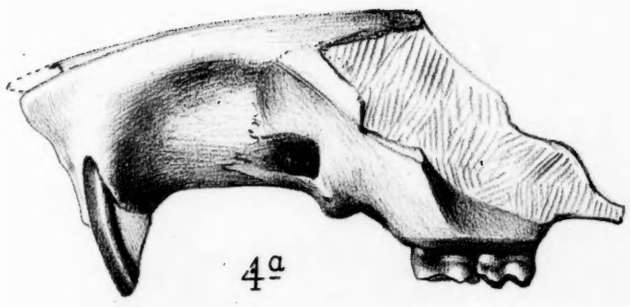

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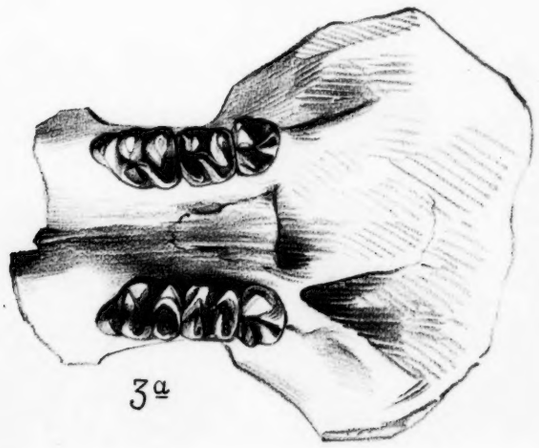

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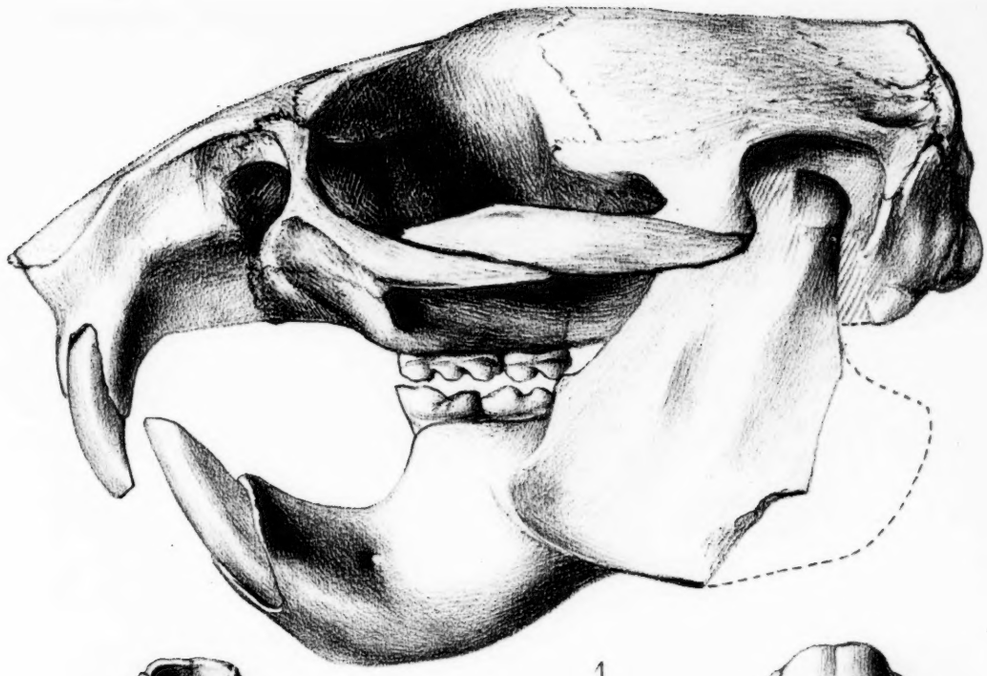
EUTYPOMYS, EUMYS, PARADJIDAUMO



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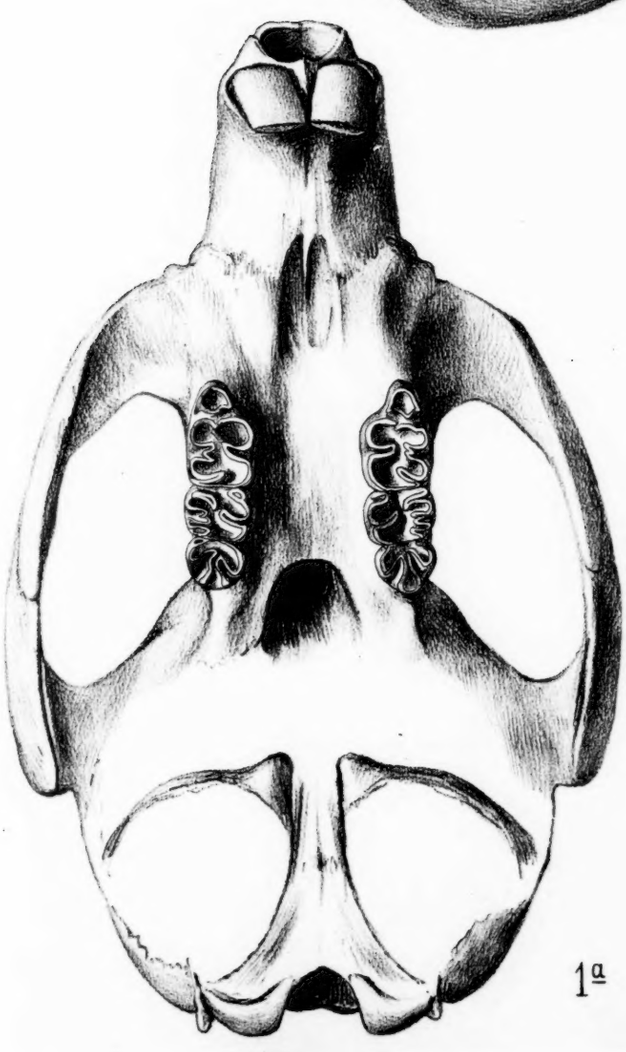

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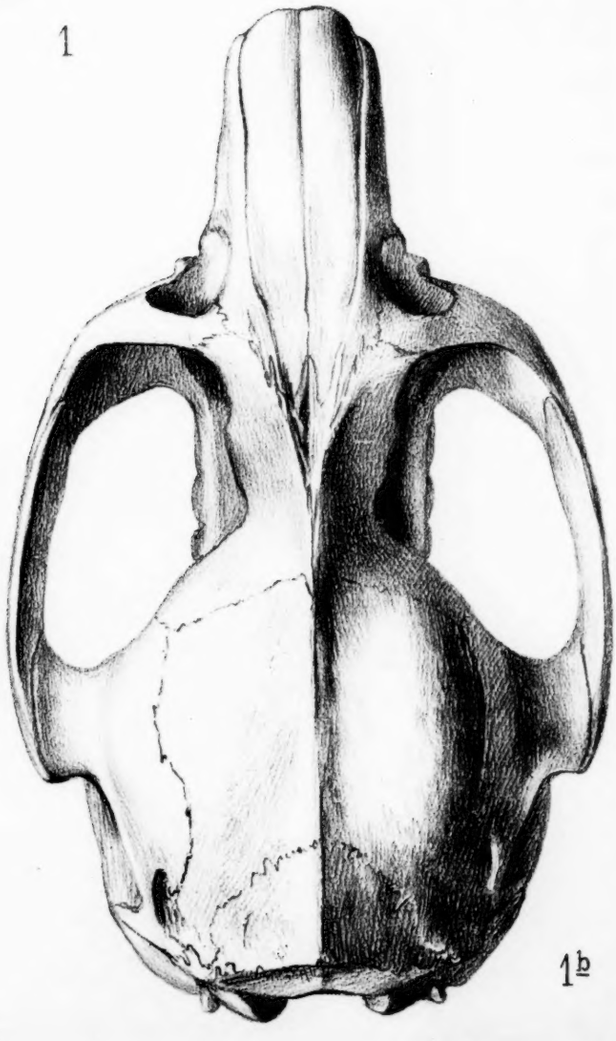

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EUMYS

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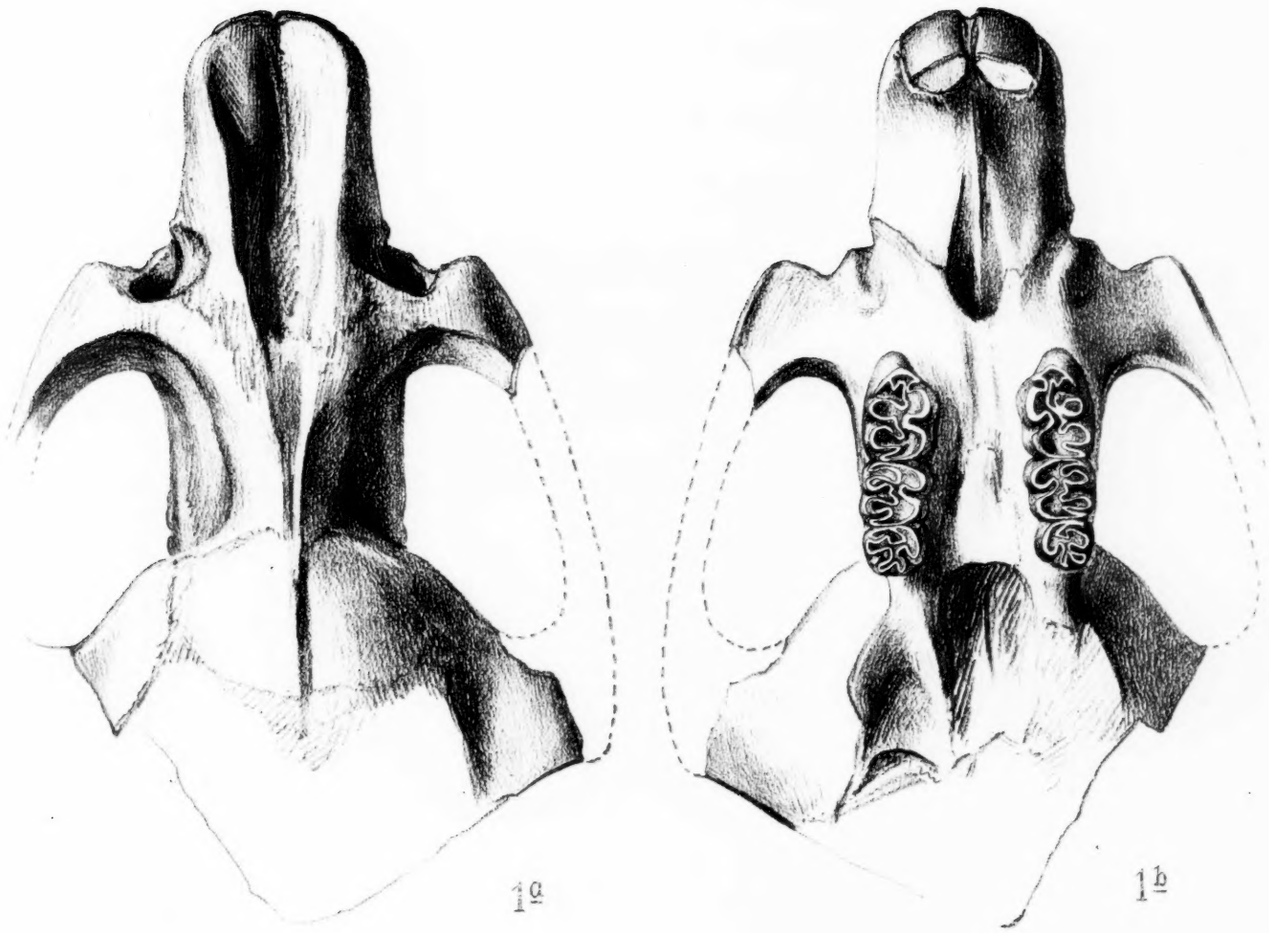

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EUMYS